The American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

Editor
John D. Mizelle, Zoology

ASSOCIATE EDITORS

Edward Albert Chapin, Washington, D. C. ..... Entomology
Albert L. Delisle, Notre Dame, Ind. ..... Plant Morphology
Carroll Lane Fenton, New Brunswick, N. J. ..... Invertebrate Paleontology
John Hobart Hoskins, Cincinnati, Ohio ..... Paleobotany
George Neville Jones, Urbana, Ill. ..... Plant Taxonomy
Remington Kellogg, Washington. D. C. ..... Mammalogy
Jean Myron Linsdale, Carmel Valley, Calif. ..... Ornithology
George Willard Martin, Iowa City, Iowa ..... Mycology
Hugh M. Raup, Petersham, Mass. ..... Plant Ecology
Karl Patterson Schmidt, Chicago, Ill. ..... Ichthyology and Herpetology
Harley Jones Van Cleave, Urbana, Ill. ..... Invertebrate Zoology

Vol. 48, 1952

(July - November)

PUBLISHED BY THE UNIVERSITY OF NOTRE DAME
NOTRE DAME, INDIANA

CONTENTS

No. 1, July, 1952

The Genus Helianthella (Compositae) ..... William A. Weber 1

Carex acutiformis in Indiana ..... F. J. Hermann 36

Notes on Wisconsin Parasitic Fungi. XV ..... H. C. Greene 37

Uniparental Miracidia of Schistosomatium douthitti and Their Progeny (Trematoda, Schistosomatidae) ..... Robert B. Short 55

Two New Species of Oochoristica from Minnesota Skunks ..... Asa C. Chandler 69

Host Relationships and Seasonal Abundance of Some Southwest Georgia Ectoparasites ..... Harvey B. Morlan 74

The Preputial Organ of Snails in the Genus Helisoma (Gastropoda: Pulmonata) ..... Emile T. Abdel-Malek 94

Records and Flower Preferences of Masarid Wasps. II. Polytropy or Oligotropy in Pseudomasaris? (Hymenoptera: Vespidae) ..... Kenneth W. Cooper 103

The Ant Larvae of the Subfamily Ponerinae—Part I ..... George C. and Jeanette Wheeler 111

Additional New Species in the Genera Anopompilinus, Anoplius, Pompilinus, and Pycnopompilus (Hymenoptera: Psammocharidae) and Corrections of Previous Papers ..... R. R. Dreisbach 145

Types and Figured Specimens of Fossil Fishes in the Patten Collection, Dartmouth College Museum, Hanover, New Hampshire ..... Robert H. Denison 161

The Relationship of the Chorus Frogs, Pseudacris nigrita feriarum and Pseudacris n. triseriata ..... Philip W. and Dorothy M. Smith 165

Evidence for Olfactory Discrimination by the Bobwhite Quail ..... Hubert Frings and William A. Boyd 181

Columbian Sharp-tailed Grouse (Pedioecetes phasianellus columbianus) in the State of Washington ..... Charles F. Yocom 185

The Foods of Fur Animals of the Patuxent Research Refuge, Maryland ..... Leonard M. Llewellyn and Francis M. Uhler 193

Ecology and Helminths of the Osage Wood Rat, Neotoma floridana osagensis, Including the Description of Longistriata neotoma n. sp. (Trichostrongylidae) ..... Melvin F. Murphy 204

Life History of the Water Shrew (Sorex palustris navigator) ..... Clinton H. Conaway 219

Notes and Discussion

Notes on Moraceae and Ulmaceae ..... Frank C. Seymour 249

The Parotid Gland of an Anteater, Tamandua tetradactyla ..... W. W. Dalquest and H. J. Warner 251

Book Reviews 252

No. 2, September, 1952

Revision of the Subfamily Leucochloridiinae Poche, 1907 (Trematoda: Brachylaemidae) ..... Irving G. Kagan 257

The Aquatic Hemiptera of Southeastern Louisiana (Exclusive of the Corixidae) ..... Leslie L. Ellis 302

The Meloidae (Coleoptera) of Texas ..... Lawrence S. Dillon 330

Immature Stages of the Marine Fly, Hypocharassus pruinosus Wh., with a Review of the Biology of Immature Dolichopodidae ..... Marion E. Smith 421

Studies of the Biology of the Cyprinid Fishes of the Chub Genus Nocomis of Northeastern United States ..... Ernest A. Lachner 433

Studies on the Lizard Family Xantusiidae I. The Systematic Status of the Baja California Night Lizards Allied to Xantusia vigilis, with the Description of a New Subspecies ..... Jay M. Savage 467

The Hair of California Mammals with Keys to the Dorsal Guard Hairs of California Mammals ..... William V. Mayer 480

No. 3, November, 1952

The Pelvic Musculature of the Loon, Gavia immer ..... Harry Hammond Wilcox 513

List of the Snakes of the United States and Canada by States and Provinces ..... A. H. Wright and A. A. Wright 574

The Ant Larvae of the Subfamily Ponerinae—Part II ..... George C. and Jeanette Wheeler 604

Mosquito Studies in the Panama Canal Zone During 1949 and 1950 (Diptera, Culicidae) ..... Stanley J. Carpenter and E. L. Peyton 673

Descriptions of New Species and Notes on North American Orthoptera ..... H. F. Strohecker 683

A New Albinistic Crayfish of the Genus Cambarus from Southern Missouri with a Key to the Albinistic Species of the Genus (Decapoda, Astacidae) ..... Horton H. Hobbs, Jr. 689

Zoogeographic Regions of Indiana ..... W. B. Barnes 694

The Vegetation of the Jackson Hole Wildlife Park, Wyoming ..... John F. Reed 700

The Effect of Precipitation and Temperature upon the Radial Growth of Red Pine ..... Robert E. Dils and Maurice W. Day 730

List of Non-Vascular Plants from Ponape, Caroline Islands ..... S. F. Glassman 735

Notes on Wisconsin Parasitic Fungi XVI ..... H. C. Greene 741

A Phenological Study of the Flora of the Chicago Region ..... Floyd A. Swink 758

Book Review 768

257
302
330
421
433
467
480
513
574
604
673
683
689
694
700
730
735
741
758
768

UNIVERSITY
OF MICHIGAN
JUL 1 1952
SCIENCE
LIBRARY

BIO

The
American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

John D. Mizelle, Editor

•

CONTENTS

The Genus Helianthella (Compositae) ... William A. Weber 1
Carex acutiformis in Indiana ... F. J. Hermann 36
Notes on Wisconsin Parasitic Fungi. XV ... H. C. Greene 37
Uniparental Miracidia of Schistosomatium douthitti and Their Progeny (Trematoda, Schistosomatidae) ... Robert B. Short 53
Two New Species of Oochoristica from Minnesota Skunks ... Asa C. Chandler 69
Host Relationships and Seasonal Abundance of Some Southwest Georgia Ectoparasites ... Harvey B. Morlan 74
The Preputial Organ of Snails in the Genus Helisoma (Gastropoda: Pulmonata) ... Emile T. Abdel-Malek 94
Records and Flower Preferences of Masarid Wasps. II. Polytropy or Oligotropy in Pseudomasaris? (Hymenoptera: Vespidae) ... Kenneth W. Cooper 103
The Ant Larvae of the Subfamily Ponerinae—Part I ... George C. and Jeanette Wheeler 111
Additional New Species in the Genera Anopompilinus, Anoplius, Pompilinus, and Pycnopompilus (Hymenoptera: Psammocharidae) and Corrections of Previous Papers ... R. R. Dreisbach 145
Types and Figured Specimens of Fossil Fishes in the Patten Collection, Dartmouth College Museum, Hanover, New Hampshire ... Robert H. Denison 161
The Relationship of the Chorus Frogs, Pseudacris nigrita feriarum and Pseudacris n. triseriata ... Philip W. and Dorothy M. Smith 165
Evidence for Olfactory Discrimination by the Bobwhite Quail ... Hubert Frings and William A. Boyd 181
Columbian Sharp-tailed Grouse (Pedioecetes phasianellus columbianus) in the State of Washington ... Charles F. Yocom 185
The Foods of Fur Animals of the Patuxent Research Refuge, Maryland ... Leonard M. Llewellyn and Francis M. Uhler 193
Ecology and Helminths of the Osage Wood Rat, Neotoma floridana osagensis, Including the Description of Longistriata neotoma n. sp. (Trichostrongylidae) ... Melvin F. Murphy 204
Life History of the Water Shrew (Sorex palustris navigator) ... Clinton H. Conaway 219
Notes and Discussion
Notes on Moraceae and Ulmaceae ... Frank C. Seymour 249
The Parotid Gland of an Anteater, Tamandua tetradactyla ... W. W. Dalquest and H. J. Werner 251
Book Reviews ... 252

Vol. 48 July, 1952 No. 1

EDITORIAL STAFF

JOHN D. MIZELLE ..... *Zoology*
Editor, University of Notre Dame, Notre Dame, Ind.

EDWARD A. CHAPIN ..... *Entomology*
U. S. National Museum, Washington, D. C.

ALBERT L. DELISLE ..... *Plant Morphology*
University of Notre Dame, Notre Dame, Ind.

CARROLL LANE FENTON ..... *Invertebrate Paleontology*
404 Livingston Ave., New Brunswick, N. J.

JOHN HOBART HOSKINS ..... *Paleobotany*
University of Cincinnati, Cincinnati, Ohio

GEORGE NEVILLE JONES ..... *Plant Taxonomy*
University of Illinois, Urbana, Ill.

REMINGTON KELLOGG ..... *Mammalogy*
U. S. National Museum, Washington, D. C.

JEAN MYRON LINSDALE ..... *Ornithology*
Hastings Reservation, Robles del Rio, Calif.

GEORGE WILLARD MARTIN ..... *Mycology*
State University of Iowa, Iowa City, Iowa

HUGH M. RAUP ..... *Plant Ecology*
Harvard Forest, Harvard University, Petersham, Mass.

KARL PATTERSON SCHMIDT ..... *Ichthyology and Herpetology*
Chicago Natural History Museum, Chicago, Ill.

HARLEY JONES VAN CLEAVE ..... *Invertebrate Zoology*
University of Illinois, Urbana, Ill.

NOTE: THE AMERICAN MIDLAND NATURALIST, published by the University of Notre Dame is primarily, though not exclusively, devoted to the Natural History of the Middle West. A wide selection of papers on botany, paleontology and zoology is published in bi-monthly issues, three of which make up a volume.

Authors are invited to submit carefully prepared manuscripts and requested to limit tables and illustrations as much as possible. Abstracts and reprint orders should accompany manuscripts or corrected proofs.

The following numbers are out of print: Vol. 1 (1, 4, 5, 8-12); Vol. 2 (1-3, 8, 9); Vols. 3, 4 (all numbers); Vol. 5 (1, 6-8); Vol. 6 (1, 5, 7-12); Vol. 7 (1, 6); Vol. 8 (2); Vol. 9 (2); Vol. 11 (1); Vol. 12 (12); Vol. 14 (1, 5-6); Vol. 15 (4); Vol. 16 (2); Vol. 17 (1, 2); Vol. 18 (1); Vol. 20 (1, 2); Vol. 21 (2, 3); Vol. 22 (1); Vols. 23-26 (all numbers); Vol. 27 (1); Vol. 36 (1); Vol. 37 (2, 3); Vol. 38 (1). Volume groups 1-12, 13-18 and 19-44 contain 12, 6 and 3 issues respectively. Available issues of Vols. 1-6 $4.00, single issues 40 cents; Vol. 7 $2.50, single issues 25 cents; Vols. 8-12 $4.00, single issues 40 cents; Vols. 13, 14 $2.50, single issues 30 cents: Vol. 15 $3.00, single issues 60 cents; Vol. 16 $4.00, single issues 75 cents; Vol. 17 $5.50, Part I, $2.50, single issues $1.25. Subscription price per year $6.00.

Inquiries concerning exchanges for specimens, journals, special volumes or duplicate books should be addressed to *The American Midland Naturalist*, Notre Dame, Indiana, where subscriptions and payments are also received. Offers should accompany requests for exchange.

Abbreviated citation: *Amer. Midl. Nat.*

The American Midland Naturalist is indexed in the INTERNATIONAL INDEX.

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103; Act of October 3, 1917, authorized on July 3, 1918.

The American Midland Naturalist

Published Bi-Monthly by The University of Notre Dame, Notre Dame, Indiana

VOL. 48 JULY, 1952 No. 1

The Genus Helianthella (Compositae)*

William A. Weber

University of Colorado, Boulder

This paper is a continuation of studies concerning certain genera of helianthoid Compositae of western North America. The discovery of the extensive occurrence of introgressive hybridization in the genera *Balsamorhiza* and *Wyethia* (Rogers, 1942; Maguire, 1942; Ownbey & Weber, 1943; Weber, 1946) and in the genus *Helianthus* (Heiser, 1947, 1949) emphasizes the need of investigations into the behavior of species in other allied genera. The present study is essentially a taxonomic and geographic one and was undertaken as a prerequisite to genetic analyses and experimental studies which are being made concerning the various genera of the tribe Heliantheae.

HISTORY

Helianthella is a small genus comprising eight species of perennial sunflowers which are indigenous to the western United States and adjacent Canada and Mexico. The genus was proposed by Torrey and Gray (1842) to include five species, two of which, *H. lanceolata* and *H. uniflora*, had been published previously in combinations under *Leighia* and *Helianthus*, respectively. The five entities of Torrey and Gray includes two species from Florida, namely, *H. grandiflora* and *H. tenuifolia*, which were grouped later under a subgenus Pseudo-helianthus (Torrey & Gray, 1884) and subsequently removed to form the genus *Phoebanthus* (Blake, 1916). A second subgenus, *Enceliopsis* (Gray, 1883), which includes a few Great Basin xerophytes with scapose stems, was raised to generic rank by Nelson (1909). The species which remain in the genus *Helianthella* as it is understood at the present time belong to the group which was referred to by Gray as "*Helianthella proper.*" The disposition of other entities which have been assigned from time to time to *Helianthella* will be found in the lists of synonyms and rejected names.

GENERIC RELATIONSHIP

Helianthella is placed in the tribe Heliantheae, subtribe Verbesininae. The combination of characteristics which separates this genus from its relatives is as follows: *Habit:* herbaceous, perennial, *Stem:* leafy, *Leaves:* the lower opposite, the upper opposite or alternate; blades simple, entire, usually strongly 3- or 5-nerved, *Flowers:* disk-flowers perfect, ray-flowers neuter, *Fruit:* strongly lateral-

* Research sponsored by the University of Colorado Council on Research and Creative Work.

ly compressed, the pappus, when present, composed of a few persistent bristles and/or low intermediate squamellae.

The technical distinctions between *Helianthella* and related genera were pointed out in a diagnostic key by *Blake* (1913). A detailed discussion of the relationships of most of these genera, not including *Helianthella,* however, is to be found in a revision of the genus *Viguiera* (Blake, 1918). Although his key is workable in most instances, two of the criteria used by Blake to distinguish *Helianthella* from its relatives do not hold for certain species. For example, the presence or absence of squamellae was used to separate *Helianthella* (squamellae present) from *Encelia, Geraea,* and *Simsia* (squamellae absent). *Helianthella castanea,* however, lacks squamellae, and in *H. californica* the squamellae are exceedingly difficult to detect. In addition, the separation of *Helianthella* from *Enceliopsis* on the basis of relative villosity of the fruit is of no value because of exceptions in *Helianthella microcephala,* in which the fruit is densely villous as in *Enceliopsis,* and *Enceliopsis grandiflora,* in which the fruit is nearly glabrous as in most species of *Helianthella.* The genera concerned are, nevertheless, amply distinct on the basis of other combinations of characters.

DISTRIBUTION

Helianthella is confined to the mountainous western half of North America and northern Central America. Its species are distributed from southern British Columbia to northern Mexico in the Rocky Mountains, intermountain plateaus, and mountain ranges of the Great Basin, and to central California in the Sierra Nevada and Coast ranges. The species replace each other geographically or ecologically; the overlapping of populations in a single area or habitat is a rare occurrence. No noteworthy concentration of species exists in any single physiographic or biotic province. Discontinuous distributions involving gaps of more than a few hundred miles do not occur.

Each species has its own distinctive distributional pattern, as follows: *H. microcephala*—Colorado Plateau Province (Map 1), *H. ciliata*—North Mexican Interior Plateau (Map 2), *H. mexicana*—Sierra Madre Oriental (Map 2), *H. uniflora*—northern Rocky Mountains, Great Basin ranges, and east slope of Cascade range (Map 3), *H. quinquenervis*—Central and southern Rocky Mountains (Maps 4 and 2), *H. Parryi*—Southern Rocky Mountains (Map 5), *H. californica*—Sierra Nevada and Coast ranges (Map 6), *H. castanea*—San Francisco Bay area (Map 7).

The areal patterns of the species illustrate several features which are worth noting. It is quite obvious, for example, that the principal mountain masses have been of great importance in providing migration routes for the species. It follows also that the arid plains or sedimentation basins which separate the mountain ranges constitute major barriers to migration. In the few instances in which two markedly discontinuous areas of a species are separated by an arid plain, it may be assumed that the occupation by the species of a continuous area antedated the formation of the trough, because long distance dispersal of *Helianthella* seed across such a barrier appears to be unlikely. Two such discontinuities are the Black Hills and Rocky Mountain areas of *H. quinque-*

nervis, which are now separated by the high plains of southern Wyoming, and the areas of *H. uniflora* which are divided by the Wyoming Desert.

In a very few instances, certain species or genera which are believed to have been derived from the mesophytic species of *Helianthella* inhabit arid troughs or plateaus in areas adjacent to the *Helianthella* range. For example, the highly xerophytic genus *Enceliopsis* replaces *Helianthella* on the hot, dry, deserts of the Great Basin. On the other hand, it is equally possible that the mesophytic species of the mountains may be derived from xerophytic types such as *H. microcephala*.* The phylogeny of the groups concerned must rest upon a sound foundation, however, before much speculation along these lines will be justified.

SPECIFIC CONCEPT

The species of *Helianthella* are morphologically discrete populations which are effectively isolated from each other by geographic barriers, spaced breeding seasons, or unique ecological requirements. Interspecific hybridization is known or suspected to occur in only one instance, and hybrid swarms have never been reported.

The genus may be broken into pairs of closely related species or vicariads, which, as a rule, inhabit adjacent areas. The two species which have nodding heads, *H. quinquenervis* and *H. Parryi*, for example, occupy adjacent areas in the Rocky Mountain system. *H. mexicana* and *H. ciliata*, with dark-colored disk-flowers, *H. californica* and *H. castanea*, with glabrous fruits, are examples of vicarious pairs, and *H. uniflora* and its variety *Douglasii* might be regarded as an incipient vicarious species pair.

NATURAL HYBRIDIZATION

Natural interspecific hybridization is extremely rare in *Helianthella*. A single instance of suspected hybridization, involving *Helianthella mexicana* and *H. quinquenervis*, has been observed. These two species occur together on the rich moist subalpine meadows near the summit of Cerro Potosí, in Nuevo Leon, Mexico. At this locality *H. quinquenervis* is at the southern limit of its range. Specimens of each species and of an obviously intermediate individual were collected on July 21, 1935, *Mueller* 2277 (*H. quinquenervis*), Aug. 16, 1938, *Schneider* 1002 (*H. mexicana*), and Aug. 3, 1938, *Univ. Ill. Mex. Biol. Exped.* 967 (intermediate). The intermediate specimens which were distributed to several herbaria (Chicago Museum of Natural History; Univ. of Arizona) appear to be divisions of a single individual plant.

On the Cerro Potosí, *H. quinquenervis* blooms in July, and *H. mexicana* blooms in the middle of August. The intermediate individual was described as just coming into bloom on August 3. The collector stated, in addition, that "so far observed [this is] a rather rare plant, restricted to moist meadows in the pine forest nearer timberline." The habitat, if accurately described, may

* After this was written, the writer obtained chromosome counts for two species of *Enceliopsis*. The haploid number, n = 18, constitutes evidence in favor of the latter hypothesis, for it is highly improbable that *Helianthella* with 15 pairs of chromosomes, could have given rise to *Enceliopsis*, with 18 pairs.

be nearly the habitat of *H. quinquenervis*. As will be shown in the table below, the individual in question resembles that species as to the majority of characters.

H. quinquenervis	*Intermediate*	*H. mexicana*
Head: large, solitary	large, solitary	small, solitary
Peduncle; nodding	nodding	erect
Leaves: acuminate	acute	acute
Petiole: elongate	none or short	none or short
Venation: 5-nerved	5-nerved	1-3-nerved
Ray-flowers: elongate	short (possibly because of immaturity)	short
Phyllaries: ovate lanceolate, drying black	lanceolate, drying green	lanceolate, drying green
Disk-flowers: yellow	yellow	brown or purple
Stem height: 5-15 dm.	1-2 dm.	1-2 dm.
Pubescence glabrate or sparsely hirsutulous	densely strigose	densely strigose

In summarizing, the intermediate individual possesses the habit, pubescence, and to some extent the leaf shape and phyllary shape of *H. mexicana*, but preserves the remaining qualitative characteristics of *H. quinquenervis*. In the absence of more detailed observations, the foregoing notes are submitted in order to record, on fair circumstantial evidence, the occurrence of a putatively hybrid individual.

ECONOMIC IMPORTANCE

The following account of the economic importance of *Helianthella* species is found in the United States Forest Service Range Plant Handbook (U.S.D.A., 1937, p. W89). "In some sections little-sunflower [*H. uniflora*] provides considerable forage. The leafage, flowers, and more tender portions of the stems are eaten by all classes of grazing animals, being fair to very good in palatability for sheep and only slightly less palatable for cattle. The flower heads are eaten with unusual relish. The foliage is utilized by all classes of grazing animals during the summer, but after drying in the fall is grazed to a less extent by livestock and game. The strong woody taproot enables this plant to stand up unusually well under heavy grazing."

MORPHOLOGY

Roots.—*Helianthella* possesses a woody or somewhat fleshy taproot, the crown of which is usually buried a few inches below the ground. The taproot bears at its apex a few short, erect underground stems (caudices).

Stems.—The stem consists of an underground perennial portion, the caudex, and an aerial annual portion. Although the caudex typically is erect, it occasionally assumes a horizontal position and may become elongated. This behavior may be the result of some disturbance of the normal orientation of the plant in the soil such as might be caused by minor landslides, erosion pressures, etc. Such caudices resemble rhizomes and may function as such.

The caudex bears a few pairs of opposite buds from which the aerial stems arise. The aerial stem is unbranched below the inflorescence and is erect throughout its development, in contrast to the situation in *Wyethia* in which the stem elongates in a horizontal position but becomes erect by bending at the base.

Leaves.—The leaves may be either cauline or basal. Basal rosettes of leaves are usually formed by buds which do not produce a flowering stem during the current season. Flowering stems rarely possess large basal leaves, although the lower pairs of cauline leaves are sometimes quite large. The leaves of the basal rosette are similar in shape, texture, and indument, to those of the stem.

The lowermost cauline leaves are always opposite, while the uppermost leaves may be alternate or opposite. In some species, leaves are occasionally produced three at a node. The leaf margins are always entire. The leaf blades are simple and range in shape from linear to ovate-lanceolate. Venation is pinnate, but most leaves appear to be triple-nerved because of the accentuation of two of the lowermost lateral nerves.

The shape, number, and relative sizes of the upper, middle, and lower cauline leaves furnish valuable taxonomic criteria, although these characters are most reliable when considered along with other diagnostic features of the inflorescence.

Indument.—All species are more or less hirsute or strigose with multicellular hairs. The pubescence is variable from species to species and from individual to individual and cannot be said to be diagnostic for any species. Furthermore, the pubescence of the foliage and the stem becomes more sparse as the organs elongate, and much of the indument is eventually lost because of breakage of the hairs. Most individuals are scabrous or glabrate at maturity; residual pubescence is most abundant at the base of the involucre.

The pubescence of the fruit, on the other hand, is quite characteristic of the species. For example, in *Helianthella microcephala* the fruits are densely appressed-pubescent, and in *H. californica* they are quite glabrous. In most species the fruits are either glabrous or are sparsely appressed-hirsute on the faces.

Inflorescence.—In most species the inflorescence is a single, terminal head. A few small axillary heads are sometimes present but these often abort before coming to full bloom. *H. microcephala* is an exception with numerous heads arranged in a corymbose cluster. The order of flowering is determinate, that is, the terminal head blossoms first. Within the heads themselves, flowering is centripetal. The heads are usually erect throughout anthesis, but a few species are characterized by having heads which are turned with the axis at right angles to the stem.

Involucre.—The involucre is hemispherical. The involucral bracts, or phyllaries, are subequal or graduated (in *H. microcephala*), erect or with spreading tips, and are arranged in approximately three series. They range

in outline from ovate and obtuse (in the above species only) to lanceolate or lance-linear with acuminate tips. In a few species the outermost phyllaries are greatly enlarged and leaf-like. In general, the pubescence of the phyllaries parallels that of the stem and leaves.

Receptacle and paleae.—The receptacle is flat or broadly convex. The receptacular paleae, or chaff, are oblanceolate, acute, conduplicate, and deciduous with the mature fruits or falling from the head soon after anthesis. Diagnostic keys to the species often employ major dichotomies which are based on the relative rigidity of the paleae, e.g. "paleae soft and weak" versus "paleae rigid." While two hardness classes may be demonstrated, these are apparent only to persons who have had considerable experience with both types. The relative rigidity of the paleae is an interesting and perhaps valid distinction between certain species, but its use as a primary key-character is not encouraged.

Corollas.—The heads possess a single marginal row of neuter, yellow ray-flowers and a central group of perfect, tubular, yellow or purplish-brown disk-flowers. Structural characteristics of the flowers are uniform throughout the genus. The disk-corollas have a narrow cylindrical tube which is slightly expanded above into a tubular-campanulate 5-lobed limb. Median vascular traces of the corolla are usually lacking. The anthers have ovate appendages and are sagittate at the base. The style branches are slender, terete or flattened and slightly expanded at the apex, and are minutely pubescent from base to apex.

Fruits.—The cypselae (fruits) of *Helianthella* are strongly laterally compressed and are oblanceolate to obcordate in outline. The pappus, when present, consists of two awns or bristles, one on each side of the apex. The apex is depressed in most species, forming an apical notch. The margins are thin or very narrowly winged. Laciniate scales (squamellae) may be present between the bristles, forming a low crown. In a few species the pappus is totally lacking. Characters of the cypsela, while they are often diagnostic, are not used in the key because the fruit is not always available for examination and because the differences are not apparent to students who do not have considerable experience with the genus.

CYTOLOGY

The chromosome numbers of six of the eight species of *Helianthella* have been determined. In each species the number was found to be $n = 15$. Chromosome counts were made at various stages in the maturation of the microspores by use of iron-aceto-carmine smear techniques. The writer wishes to acknowledge the aid of Dr. Marion S. Cave, Dr. Marion Ownbey, and Mr. James Brewbaker, who provided materials or who, for a few species, made the actual chromosome counts.

A tabular arrangement of the chromosome numbers and citations of specimens follows:

Species	n	Source
H. californica	15	burned over area in hills s.e. of Santa Rosa, Sonoma Co., Calif., Mar. 25, 1948, *Cave* 4821.
H. castanea	15	Bear Cr. road near Orinda road, Contra Costa Co., Calif., May 8, 1948, *Cave.*
H. microcephala	15	grown in garden, from plants taken at Dinosaur Nat. Mon. Hdq. area, Uintah Co., Utah, May 3, 1951, *Weber.*
H. quinquenervis	15	grassy meadow under aspens, Eldora, Gilpin Co., Colorado, July 3, 1948, *Weber* 4231.
H. Parryi	15	Rocky Mt. Forest & Range Exp. Sta., n. of Woodland Park, Teller Co., Colorado, July 9, 1949, *Weber* 4932.
H. uniflora var. *Douglasii*	15	3 mi. s. of Asotin, Asotin Co., Wash., May 30, 1948, *Ownbey* 3157; 2.5 mi. n.w. of Colton, Whitman Co., Wash., May 30, 1948, *Ownbey* 3151.

Herbarium specimens representative of the populations from which chromosome counts were obtained have been deposited in the University of Colorado Herbarium.

It is noteworthy that the genera of Heliantheae thus far studied by Weber, Heiser, and others, are homogeneous as to chromosome number within the genus, and are demonstrative of a descending aneuploid series in which the supposedly primitive genus *Wyethia* heads the list with n = 19, followed by *Enceliopsis* (unpublished), n = 18, *Helianthus*, n = 17, and *Helianthella*, n = 15.

PHYLOGENY

The linear arrangement of the species in the following taxonomic treatment is frankly artificial, since none of the species demonstrate manifestly primitive or advanced character combinations. Moreover, at the present time much of the speculation in phylogenetic trends in the Compositae is based on threads of evidence too slender to justify such sweeping generalities as the following: "In Compositae, similarity of all flowers in the head is considered a more primitive arrangement than that indicated by the presence of distinctive marginal or ray flowers" (Stockwell, 1940). This may be true in the most primitive groups of Compositae, but in the Heliantheae we may be dealing with a group in which any species having short or abortive ray-flowers may with equal justification be held to have been derived from forms with ray-flowers.

A second dictum (Bessey, 1915) holds that "the simple, unbranched stem is an earlier type, from which branching stems have been derived." This viewpoint is supported by the situation in *Crepis*, in which "primitive species are robust perennials with . . . few large flower heads" (Babcock, 1949). It does not follow, however, that all Compositae which have solitary heads are

primitive in this respect. In *Helianthella*, at least, the species with solitary heads often bear vestigial heads in the axils of the upper leaves. Such vestigial heads will develop normally if the terminal head is removed and its inhibitory effect on the axillary heads nullified. Thus, in this genus there is some justification for the belief that species with numerous heads, such as *H. microcephala*, may be more primitive in this character than those species with solitary heads.

The writer wishes to offer for what they may be worth, the following possible character-trends from generalized to specialized conditions in *Helianthella*. It should be emphasized, however, that these hypotheses apply to this genus alone.

1. Graduated phyllaries are primitive because a spiral arrangement of parts is believed to be more primitive than a compressed spiral, or cyclic arrangement. Subequal and obgraduate bracts are advanced.

2. The leafy stem is more primitive than the stem with the cauline leaves reduced or modified to form bracts.

3. Heads with well-developed ray-flowers are more primitive than heads with small or abortive ray-flowers.

4. The inflorescence of numerous heads is more primitive than the inflorescence of a single or few terminal or subterminal heads with suppressed heads below.

5. The 3-nerved condition of the leaf-blades is more primitive than the condition in which all but the median nerves are suppressed.

TAXONOMY*

HELIANTHELLA Torrey & Gray

Helianthella T. & G., Fl. N. Am. 2: 333. 1842.

Perennial herbs with stout taproots; stems several, from woody caudices, leafy, usually hirsute, becoming scabrous in age; enlarged basal leaves present or absent; leaves simple, entire, usually three-nerved, linear to lanceolate, elliptic, oblong, or ovate-lanceolate, at least the lowermost opposite; heads radiate,

* The herbaria from which material has been available for study and from which specimens are cited in this treatment are indicated by the following abbreviations: ARIZ—University of Arizona Herbarium; CA—California Academy of Sciences Herbarium; CL-UC—Ira W. Clokey Herbarium, University of California, Berkeley; CO—University of Colorado Herbarium; D—Dudley Herbarium, Stanford University; F—Chicago Natural History Museum Herbarium; FC—Colorado A. & M. College Herbarium; FS—United States Forest Service Herbarium; G—Gray Herbarium, Harvard University; IS—Iowa State College Herbarium; M—Missouri Botanical Garden Herbarium; NMX—New Mexico State College Herbarium; NY—New York Botanical Garden Herbarium; OSC—Oregon State College Herbarium; P—Pomona College Herbarium: PA—Academy of Natural Sciences of Philadelphia Herbarium; PAR—C. C. Parry Herbarium, Iowa State College; PO—University of Idaho Herbarium, Pocatello; RM—Rocky Mountain Herbarium, University of Wyoming; UAC—Intermountain Herbarium, Utah State Agricultural College; UC—University of California Herbarium, Berkeley; UO—University of Oregon Herbarium; US—United States National Herbarium; UW—University of Washington Herbarium, Seattle; WS—State College of Washington Herbarium.

usually solitary and long-peduncled, 1-4 cm. broad exclusive of ray-flowers, terminal or terminating the main branches; involucre hemispherical, the phyllaries linear-lanceolate to ovate, subequal or in one species graduate, the outermost often greatly enlarged and leaf-like; ray-flowers neuter, yellow; disk-flowers perfect, yellow, purple, or brownish-purple; receptacle flat or convex, with chaffy or chartaceous, deciduous paleae which slightly enfold the fruits; cypsela strongly laterally compressed, thin-edged or slightly wing-margined, cuneate-obovate to obcordate in outline, variously pubescent to glabrous; pappus consisting of a pair of slender persistent awns and a crown of short, lacerate squamellae, or lacking. Anthesis vernal and early aestival.

Type species: Helianthella uniflora (Nutt.) T. & G.

KEY TO THE SPECIES

A. Heads numerous (5 to many) in a corymbose inflorescence; phyllaries triangular-ovate, strongly graduate in several series, acute-tipped; ray-flowers very short, inconspicuous, little exceeding the disk; disk-flowers purple .....1. *H. microcephala*

AA. Heads few (1 to 3 well-developed); phyllaries lanceolate or lance-linear, subequal, or the outer larger, acuminate; ray-flowers ample, showy, usually greatly exceeding the disk; disk-flowers purple or yellow.

B. Disk-flowers purple; species exclusively Mexican.

C. Internodes very short, the cauline leaves longer than their internodes; involucre 2 cm. wide; ray-flowers 1.5-2.0 cm. long. Mexican Plateau species .....2. *H. ciliata*

CC. Internodes longer than the cauline leaves; involucre 1.0-1.5 cm. wide; ray-flowers less than 1 cm. long. Sierra Madre Oriental .....3. *H. mexicana*

BB. Disk-flowers yellow; species of United States and Canada, one species (No. 5) entering northern Mexico.

D. Heads stiffly erect at anthesis and afterwards; receptacular paleae firm-chartaceous.

E. Lowermost cauline leaves or basal leaves largest, the cauline leaves reduced upwards; plants of California and southwestern Oregon.

F. Involucre 1.5-2.0 (rarely up to 2.5) cm. broad; outer phyllaries rarely enlarged, not curved over the disk at maturity; cypsela strongly-compressed. Sierra Nevada and Coast ranges .....7. *H. californica*

FF. Involucre 2.5-4.0 cm. broad; some of the outer phyllaries usually very much enlarged, leaf-like; phyllaries curved over the disk at maturity; cypsela plump. San Francisco Bay area .....8. *H. castanea*

EE. Middle cauline leaves largest, the cauline leaves reduced above and below. Rocky Mountains, Great Basin ranges, and Intermountain Plateaus .....4. *H. uniflora*

DD. Heads turned to the side or nodding at anthesis and afterwards; receptacular paleae soft-scarious.

G. Plant 4 dm. tall or less; leaves spatulate or oblanceolate, usually obtuse at apex, thin-textured, rough-pubescent; involucre small (1.5-2.0 cm. broad), the ray-flowers pale yellow (intensifying on drying) .....6. *H. Parryi*

GG. Plant usually over 4 dm. tall; leaves acuminate at both ends, broadest at the middle, leathery-textured; involucre large (4-5 cm. broad), the ray-flowers bright yellow .....5. *H. quinquenervis*

1. HELIANTHELLA MICROCEPHALA (A. Gray) A. Gray

Encelia microcephala A. Gray in Proc. Amer. Acad. 8: 657. 1873. *Helianthella microcephala* A. Gray in Proc. Amer. Acad. 19: 10. 1883. *Helianthella scabra* Payson in Bot. Gaz. 80: 382. 1913.

Stem 2-6 dm. tall, leafy, unbranched below, the heads numerous, corym-

bosely arranged at the ends of long, slender, ascending branches which arise from the middle and upper nodes; plant appressed-hispidulous, with resin droplets interspersed among the hairs, becoming ciliate or scabrous in age: basal leaves numerous, linear-spatulate to very broadly spatulate, obtuse, tapering to elongate petioles; cauline leaves reduced, narrower, almost sessile; heads 1 cm. broad and high; phyllaries strongly graduate in about 3 rows, broadly oblanceolate, obtuse; paleae rigid but weak, obtuse; disk-corollas 6 mm. long, the lobes purple or brown; ray-flowers 10-13 mm. long, inconspicuous; cypsela at maturity 3 to 4 times as long as the awns, not strongly compressed, the faces densely covered by long, appressed, white hairs; intermediate squamellae well-developed; cypsela oblong, scarcely winged, faintly notched at the summit, 7-8 mm. long exclusive of the pappus.

Type locality.—"Sierra Abayo, New Mexico? Dr. Newberry in McComb's Expedition." This is the Sierra Abajo of central San Juan County, Utah.

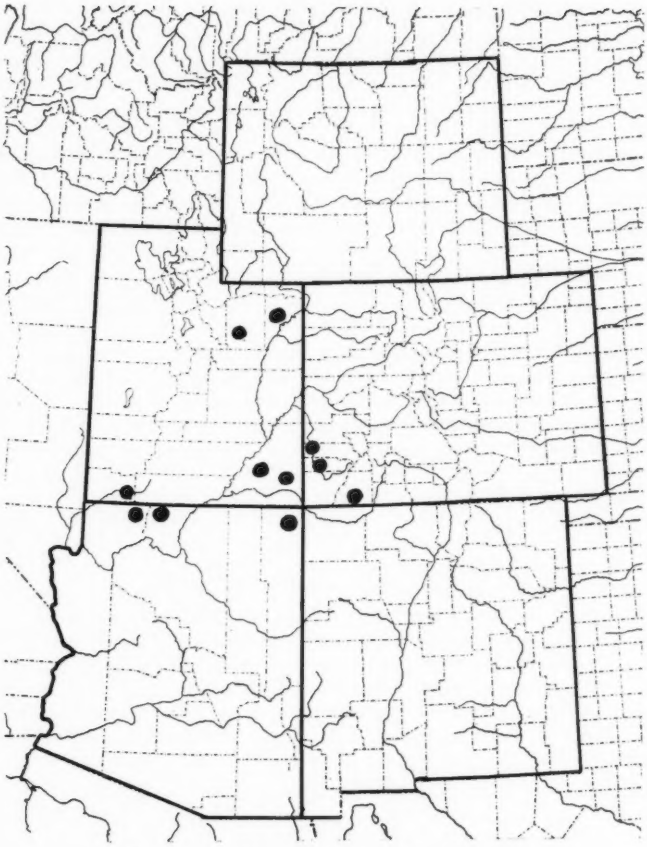
Distribution.—Gulches, ravines, and hillsides, semi-desert sites in the piñon-juniper association, 1500-2500 m. alt., Colorado Plateau province of eastern and southwestern Utah, adjacent northern Arizona, and southwestern Colorado. Blooms in August. (Map 1)

Arizona. APACHE CO.: Carrizo Mts., *Standley* 7350 (Kearney & Peebles, Fl. Ariz., published report, 1942). COCONINO CO.: 2.5 mi. n. of Fredonia, 1750 m. alt., with juniper and black sage, Aug. 9, 1945, *Hester* 1026 (ARIZ, CA). MOHAVE CO.: heavy clay soil, piñon-juniper, 1530 m. alt., 9 mi. w. of Pipe Springs, Aug. 17, 1946, *Parker, McClintock, & Robbins* 6246 (ARIZ, UC).

Colorado. DOLORES CO.: barren soil, boundary Montezuma N. F., T. 39 N., R. 14 W., ca. 20 mi. n. of Dolores, Aug. 26, 1937, *Ownbey* 1476 (CO, G, M, NY, RM, UAC, UC, WS). LA PLATA CO.: piñon-juniper hill 3 mi. n. of Ignacio, Aug. 13, 1937, *Ownbey* 1434 (ARIZ, CL-UC, CO, D, FS, G, M, NY, RM, UAC, UC, UW, WS). MONTROSE CO.: dry hills and gulches, 1800 m. alt., Naturita, Aug. 11, 1914, *Payson* 591 (RM type, CO, D, F, G, IS, M, WS, isotypes of *H. scabra* Payson); same locality, Aug. 26, 1924, *Payson & Payson* 4218 (D, G, RM, UC, US); limy shale, 2000 m. alt., among piñon-juniper, 16 mi. s. of Delta, Aug. 21, 1937, *Rollins* 1948 (D, G, M, NY, UAC, UC, US).

Utah. DUCHESNE CO.: 4 mi. w. of Duchesne, 2300 m. alt., Sept. 2, 1938, *Harrison & Garrett* 8882 (UC). SAN JUAN CO.: occasional on loose sands, forming clumps, 5 mi. n.w. of Edwin Natural Bridge, 2060 m. alt., Sept. 14, 1939, *Cutler* 3054 (G, M, NY); near Blanding, Sept. 15, 1938, *Eastwood & Howell* 6750 (CA); Sierra Abayo, Aug. 16, 1859, *Newberry* (G type, NY, US, isotypes); Armstrong and White canyons near the natural bridges, 1600-1800 m. alt., Aug. 4-6, 1911, *Rydberg & Garrett* 9470 (G, M, NY, RM, UC); dry rocky hills, Geyser Basin, July 30, 1912, *Walker* 367 (G, M, NY, P, RM, US, WS). UINTAH CO.: mountain slopes above Vernal-Manila hwy., 2 mi. n. of Vernal, July 25, 1938, *Garrett* 7861 (D, F); just below Diamond Valley, 16 mi n. of Vernal, 2150 m. alt., Aug. 20, 1936, *Noble & Andrews* (UAC, UC, UW). WASHINGTON CO.: Clear Creek, Zion N. P., Sept. 8, 1938, *Eastwood & Howell* 6365a (CA, UAC, US). COUNTY UNCERTAIN: Rabbit Valley, 2300 m. alt., Aug. 6, 1875, *Ward* 524 (F, G, PA, US).

Helianthella microcephala varies from the usual floral and vegetative patterns of *Helianthella* in the direction of the group of species in the genus



Map 1.—Distribution of *Helianthella microcephala*

Helianthus to which belong *H. occidentalis*, *H. rigidus*, and *H. atrorubens*. The phyllaries are strongly graduated, oblanceolate, obtuse, abruptly pointed; the heads are numerous, corymbosely arranged; the disk-flowers are purple; the basal leaves tend to be conspicuously enlarged, and the cauline leaves are strongly reduced. This combination of characters is anomalous in *Helianthella*, but it is the rule in the *Helianthus* species mentioned above. Furthermore, the cypselae of *H. microcephala* are not as strongly flattened or as distinctly obcordate as in the other *Helianthella* species, are scarcely wing-margined, have very highly developed intermediate squamellae, and are cov-

ered by a dense pubescence unlike that of any other species. Certain of these characteristics suggest affinities with *Wyethia*, particularly the desert species *W. scabra*, or with *Enceliopsis*. *Helianthella microcephala*, therefore, occupies a pivotal position in the genus; further study of this species may provide important keys to the problem of interrelationships among the allied genera.

Payson's *Helianthella scabra* falls well within the range of variation of *H. microcephala* and the characters (larger size, longer ligules, and "different" character of the pappus) used by that author to separate the species are not consistently diagnostic.

2. HELIANTHELLA CILIATA Blake

Helianthella ciliata Blake in Jour. Wash. Acad. Sci. 27: 383. 1937.

Stems few, erect, curved at the base, 25-40 cm. tall, from short caudices; lower leaves (2-4 pairs) opposite, the others alternate; internodes very short (3-20 mm. or rarely as much as 30 mm. long); cauline leaves about 20 in number, the middle and upper leaves 2.5-5.0 cm. long, 5-15 mm. wide, the middle stem leaves largest, the upper leaves gradually decreasing in size, the lower leaves much reduced, oblanceolate, about 1 cm. long; leaf apex usually obtuse, the base tapering to a very short or obsolete petiole, the blades 3- or obscurely 5-nerved; foliage pubescent principally along the margins and on the veins, tuberculate hispid-ciliate, almost glabrous on the leaf surfaces; head solitary, terminal, erect, on a peduncle 1-4 cm. long; involucre 10 mm. high, 2 cm. wide (as pressed), the phyllaries loosely spreading, 1.2-2.0 mm. wide at the base, acuminate, ciliate-margined, otherwise glabrate; ray-flowers oval or oblong, rather deeply and irregularly 2-3-toothed, 1.5-2.0 cm. long, 5-9 mm. wide; disk-flowers purple on the teeth, 5 mm. long; paleae soft and thin, about 8 mm. long; cypselae (immature) obovate, flattened, 3 mm. long, 1.7 mm. wide, narrowly wing-margined, emarginate, ciliate, pilose on the faces; pappus squamellae about 3-4 on each side of the cypsela, deeply laciniate, connate at base, 1.0-1.3 mm. long, equalling or exceeding the long hairs at summit of cypsela.

Type locality.—Majalca, Chihuahua, Mexico. According to García Cubas (1898), Majalca is a rancho in the district of Iturbide, about 55 kilo. (34 mi.) northwest of the provincial capitol, Chihuahua City.

Distribution.—North Mexican Interior Plateau. Known only from the type locality; ecological niche not recorded. (Map 2)

Mexico.—CHIHUAHUA: Majalca, Sept. 6, 1935, *LeSueur* 156 (type, No. 837163, in herb. Chicago Nat. Hist. Mus.; photo and fragm., US); same locality, Aug. 18-20, 1935, *LeSueur* 157 and 244 (F).

This species is characterized by its short internodes, numerous cauline leaves which exceed the internodes in length, and the dark-colored disk-flowers. As Blake stated in the original description, *H. ciliata* is obviously related to *H. mexicana*, the latter differing in having enlarged basal leaves, fewer cauline leaves, and longer internodes.

3. HELIANTHELLA MEXICANA A. Gray

Helianthella mexicana A. Gray in Proc. Amer. Acad. 15: 37. 1879.

Stems few, slender, 10-20 cm. tall, from slender caudices; basal leaves 4-5 times as long as cauline leaves; leaves all linear, 1-9 mm. wide, 5-175 mm. long, all but the lowermost alternate, progressively reduced in size upwards on the stem, 1-nerved, the lateral nerves suppressed; foliage sparsely hirsute; head solitary, erect, a few lateral heads often present but undeveloped; involucre small, 1.0-1.5 cm. wide, the phyllaries lax, lance-linear, attenuate, subequal; ray-flowers less than 1 cm. long, yellow; disk-flowers purple or brownish-purple; mature cypselae not available; immature cypselae villous on face and margin.

Type locality.—"In the Valley of Mexico, July, No. 463." The species was first collected by Parry and Palmer at "22 degrees Lat., 2000-2600 m. alt., 1878," in the province of San Luis Potosí.

Distribution.—The species proper is endemic in the province of San Luis Potosí, Mexico. The variety *latifolia* replaces it in the northern provinces of Coahuila, Nuevo Leon, and Tamaulipas. The species appears to follow the Sierra Madre Oriental, but detailed information with regard to the ecological niche occupied by the San Luis Potosí race is not available. (Map 2)

Mexico.—SAN LUIS POTOSÍ: Mt. Aguila, Charcas, July-Aug., 1934, *Lundell* 5387 (ARIZ, US); 22 degrees Lat. 2000-2600 m. alt., 1878, *Parry & Palmer* 463 (G type, F, M, PAR, US, isotypes); in mountains, San Miguelito, Aug., 1876, *Schaffner* 304 (G, NY, US).

3a. **Helianthella mexicana** var. **latifolia** var. nov.

Folia elliptica vel oblanceolata, 3-nerviis, apice acuto vel rotundo, foliis basalibus quidem in tenues petiolos usque ad dimidiatam longitudinem laminae coarctatis; folia et phyllaria aequaliter strigosa vel exemplis ultimis villosa, praecipue in basi capituli, ipsa senescente ciliata, scabrosa, vel glabrata.

Leaves elliptic or oblanceolate, 3-nerved, acute or rounded at the apex, at least the basal leaves narrowed to slender petioles as much as one-half the length of the blades; leaves and phyllaries uniformly strigose or in extreme forms villous, especially at the base of the head, becoming ciliate, scabrous, or glabrate in age.

Type locality.—San Francisco Canyon, ca. 15 mi. s.w. of Pueblo Galeana, 2500-2600 m. alt., Sierra Madre Oriental, Nuevo Leon, Mexico.

Distribution.—Open pine forests and mountain meadows, 2500-3000 m. alt., Sierra Madre Oriental in Coahuila, Nuevo Leon, and Tamaulipas provinces, Mexico. One collection (*Stanford et al.* 654) was made on limestone ridges. (Map 2)

Mexico.—COAHUILA: burned-off land with juniper and arbutus present, south slope of mountain 24 kilo. n.w. of Fraile, 2900 m. alt., July 15, 1941, *Stanford, Retherford, & Northcraft* 398 (ARIZ, D, M, NY, UW); canyons and elevated portions of Sierra Madre, 12 to 14 leagues south of Saltillo, July 25, to Aug. 1, 1880, *Palmer* (F, G, NY, PA, PAR, US). NUEVO LEON: dry, open pine forest, 3300 m. alt., Hacienda La Jolla, on Cerro Potosí, Municipio de Galeana, Aug. 16, 1938, *Schneider* 1002 (ARIZ, CL-UC, F, G, M, NY); scattered in open wood, San Francisco Canyon, ca. 15 mi. s.w. of

Map 2.—Distribution of the Mexican species of *Helianthella*. Solid circles, *H. quinquenervis* (see also map 4); solid triangles, *H. mexicana;* open triangles, *H. mexicana* var. *latifolia;* crossed circle, *H. ciliata.*

Pueblo Galeana, 2500-2600 m. alt., Sierra Madre Oriental, May 14, 1934. *Mueller & Mueller* 353 (G type, F isotype); dry mesa, 1800 m. alt., Municipality of Galeana, July 30, 1939, *Chase* 7675 (G). TAMAULIPAS: 4 kilo. w. of Miquihuana on limestone ridges in open pine forest, 3100 m. alt., Aug. 4, 1941, *Stanford, Retherford, & Northcraft* 654 (ARIZ, D, G, M, NY, UC, UW); mountain meadow 6 kilo. w. of Miquihuana, 2940 m. alt., Aug. 6, 1941, *Stanford, Retherford, & Northcraft* 738 (ARIZ, D, G, M, NY, UC, UW).

4. HELIANTHELLA UNIFLORA (Nuttall) Torrey & Gray

Helianthus uniflorus Nuttall in Jour. Acad. Sci. Phila. 7: 37. 1834. *Leighia uniflora* Nuttall in Trans. Amer. Phil. Soc. II. 7: 364. 1841. *Leighia lanceolata* Nuttall, l.c. p. 365. *Helianthella uniflora* Torrey & Gray, Fl. N. Amer. 2: 334. 1842. *Helianthella lanceolata* Torrey & Gray, *op. cit.*, p. 334. *Helianthella multicaulis* D. C. Eaton,, Bot. King's Exped. 5: 170. 1871.

Stem 4-12 dm. high, somewhat hirsute throughout or merely puberulent, becoming scabrous in age, simple or sparingly branched above; leaves lanceolate to elliptic, rarely ovate; enlarged basal leaves absent, the cauline leaves in 3-6 opposite pairs, the middle pairs largest, 3-nerved from below the middle, obtuse to acute at the apex, short-petioled or sessile, the blades 12-25 cm. long, the upper sessile; head erect, terminal, solitary, a few suppressed lateral heads often present; involucre 12-18 mm. high, 1.5-2.0 cm. broad, the phyllaries subequal, appressed, lanceolate-attenuate, the outermost frequently elongated and leaf-like, uniformly cinereous-pubescent, drying green; receptacular paleae

rigid; ray-flowers chrome-yellow, 1.5-3.0 cm. long; disk-flowers yellow; cypsela 6-7 mm. long, narrowly obovate, ciliate above, appressed-pubescent on the lateral faces; pappus of two slender awns, 3.5-4.0 mm. long, the intermediate squamellae short or obsolete.

Type locality.—"On the borders of the upper branches of the Columbia," collected by Wyeth. The writer has examined a photograph of the type specimen (Herb. British Museum) and an isotype (Gray Herb.) annotated in Nuttall's hand "Helianthus* uniflorus (Nutt. fr. Wyeth) Waters of Columbia." Photographs of the same specimen which were distributed to various herbaria by Blake bear an incorrect recent annotation to the effect that the specimen was collected by Nuttall in the Rocky Mts. These photographs are very poor and do not reproduce the original label, which bears the correct collection data.

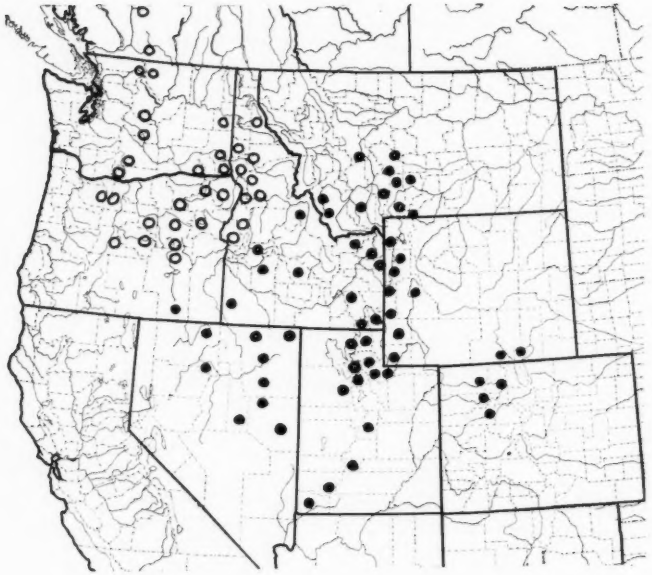
The original label on the type specimen, fortunately, bears the date of collection, June 9. The year 1833 is implied by the remainder of the collection data, for on the corresponding dates in 1832, and in 1834, Wyeth was travelling in the area drained by the North Platte River rather than the Columbia.

Having ascertained the date of collection, the type locality may be determined by consulting the Wyeth Journals (Young, ed., 1889). From June 2, to the beginning of July, 1833, Wyeth camped in the vicinity of the lava beds and Camas Prairie, between the headwaters of the Salmon River and the Snake River, in what is now east-central Idaho. Thus, Wyeth's "upper branches of the Columbia" were, in this instance, that river's southeastern tributaries. A study of Wyeth's notes, which include estimates of travel mileage as well as estimates of distances from such well-known landmarks as the "Three Butes" [Twin Buttes and Cinder Cone, 25 mi. w. of Idaho Falls,] "Trois Tetons" [Grand Tetons,] etc., places the type locality near the "sinks of Little Lost River or Birch Creek, on the western border of the lava beds along what is now the boundary between Jefferson and Butte counties, in east central Idaho.

Distribution.—Rocky Mountains, Intermountain plateaus, and ranges of the Great Basin, from southern Idaho, southeastern Oregon, and southwestern Montana southward to northern Nevada, southern Utah, and northwestern Colorado. The species proper is replaced north of this area by its variety *Douglasii*. *Helianthella uniflora* grows in a wide variety of habitats, such as sagebrush summits, swales, grassy hillsides, openings in aspen forests, steep, rocky slopes, and spruce-fir forests, from 1500 to 3400 m. alt. Blooms in June and July. (Map 3)

Colorado. GARFIELD CO.: aspens, upper middle fork of Stuart Creek, 2500 m. alt., July 18, 1935, *Graham* 9732 (CL-UC, G, M). MOFFAT CO.: Price Creek, 2300 m. alt., July 9, 1936, *Nielson* 30 (FS). RIO BLANCO CO.: Aldrich Lake, 2250 m. alt., July 22, 1937, *Johnson* 716 (CO); low hills in *Artemisia*, sandy clay loam 15 mi. s. of Meeker, July 22, 1935, *Maguire, Piranian, & Richards* 12898 (UAC); Burro Mts., July 31, 1915, *Sturgis* (G). ROUTT CO.: T. 9 N., R. 87 W., 2600 m. alt., Routt N. F., July 20, 1932, *Towne* 61 (FS); Steamboat Springs, July 25, 1891, *Crandall* 471 (FC, US).

Idaho. BANNOCK CO.: Camp Tendoy, near Pocatello, July 23, 1936, *Cronquist* 318-36 (UAC). BEAR LAKE CO.: stony, moist slopes, 1980 m. alt., Montpelier, July 9,



Map 3.—Distribution of *Helianthella uniflora* (solid circles) and *H. uniflora* var. *Douglasii* (open circles)

1911, *Nelson & Macbride* 1041 (D, F, G, M, NY, P, RM, UAC UC, US). BLAINE Co.: stony ridges on the bottomlands, Ketchum, 1960 m. alt., *Nelson & Macbride* 1207 (D, F, G, M, NY, P, RM, UAC, UC, US); South Boise River, 7 mi. above Shake Creek R. S., 1600 m. alt., June 25, 1913, *Woods* 359 (FS, RM). BOISE Co.: moist gully, Clear Creek, T. 10 N., R. 8 E., July 10, 1940, *Davis* 2748 (CL-UC, PO, UAC); dry, gravelly soil 3 mi. e. of Lowman, July 10, 1944, *Hitchcock & Muhlick* 9757 (G, PO, RM, UAC, UW, WS). BUTTE Co.: foothills at edge of desert at Martin. 1900 m. alt., June 14, 1941, *Cronquist* 2358 (M, PO, UAC). CLARK Co.: swale 4 mi. n e of U. S. Sheep Sta., July 4, 1937, *Cronquist* 665-37 (UAC, UC); deep clay loam, T. 11 N., R. 37 E., Sec. 11, Dubois, 2000 m. alt., June 25, 1934, *Pechanec* 21 (FS, PO). ELMORE Co.: moist soil, Trinity Lake, T. 3 N., R. 9 E., July 20, 1940, *Davis* 2852 (PO, UAC); open grassy hillside just n. of Atlanta-Featherville Road summit, vicinity of Bald Mt., July 23, 1944, *Hitchcock & Muhlick* 10229 (CA, G, PO, RM, UAC. UW, WS); south slope, Trinity Mt., 2 mi. s. of Trinity Lakes, ca. 10 mi. w. of Featherville, July 25, 1944, *Hitchcock & Muhlick* 10384 (NY, UAC, UW, WS). FRANKLIN Co.: Hillyard Cr., Divide, Aug. 11, 1941, *Davis* 3970 (PO). FREMONT Co.: along Buffalo River at Yellowstone hwy., 2100 m. alt., July 12, 1939, *Cronquist* 1635 (M. PO, UAC); along railroad tracks between Ashton and St. Anthony, 1600 m. alt., July 25, 1939, *Cronquist* 1764 (M, PO, UAC). LEMHI Co.: Big 8 Mile, 2260 m. alt., Salmon N. F., July 16, 1931, *Phillips* 70 (FS). TETON Co.: Moose Creek, July 12, 1934, *Christ* 5158 (US); sagebrush country, Victor, July, 1912, *Eikenberry* 2 (F). OWYHEE Co.: hillsides, 2300 m. alt., Silver City, July 23, 1910, *Macbride* 457 (D, F, G. M, NY, RM, UC, US, WS); steep, stony hills, House Creek, June 29, 1912, *Nelson & Macbride* 1797 (G, RM, US).

Montana. BEAVERHEAD CO.: meadow 20 mi. from mouth of Wise River, Aug. 2, 1946, *Hitchcock & Muhlick* 15251 (UW); open gravelly bank, Vipont Park, e. of Sheep Mt., Pioneer Range, July 31, 1945, *Hitchcock & Muhlick* 13009 (RM, UAC, UW, WS); grassy, rocky slopes ca. 25 mi. w. of Dillon in pass to Big Hole Valley, July 20, 1945, *Hitchcock & Muhlick* 12565 (CO, OSC, RM, UAC, UW, WS) GALLATIN CO.: Bridger Creek Basin, 1700 m. alt., July 17, 1905, *Blankinship* 271 (F, PA, US); Spanish Basin, 2100 m. alt., June 28, 1897, *Rydberg & Bessey* 5178 (F, G, NY, PA, RM, US); Wallrock Basin, 12 mi. n.w. of Wilsall, July 12, 1921, *Suksdorf* 484-M (WS); Bridger Pass, July 22, 1921, *Suksdorf* 566-M (WS). LEWIS & CLARK CO.: Helena, July 19, 1891, *Kelsey* (D, P). MADISON CO.: T. 10 S., R. 3 W., Sec. 11, n. of Cottonwood River, 2300 m. alt., Vigilante Experimental Range, July 3, 1936, *Dobrinz* 49 (FS); 2 mi. s.w. of Brandon Lakes, Tobacco Root Mts., July 29, 1947, *Hitchcock* 16966(UC). MEAGHER CO.: Little Belt Mts., near the pass, 2300 m. alt., Aug. 10, 1896, *Flodman* 871 (M, NY, US); open sagebrush hills 7 mi. s.w. of Ringling, July 17, 1945, *Hitchcock & Muhlick* 12430 (OSC, RM, UAC, UW, WS). PARK CO.: north slope of Baldy Mt., Absaroka Range, 1900 m. alt., June 25, 1912, *Eggleston* 8109 (US); Cooke City, 2500 m. alt., Aug. 16, 1924, *Pearson & Pearson* 144 (RM); Suksdorf Gulch, 9 mi. n.w. of Wilsall, July 29, 1921, *Suksdorf* 639-M (WS). SWEETGRASS CO.: dry roadside, foothills of Crazy Mts., along Timber Creek, Aug. 6, 1945, *Hitchcock & Muhlick* 13332 (RM, UAC, UW, WS).

Nevada. ELKO CO.: Wm. Smiley Ranch near Deeth, 1900 m. alt., July 20, 1908, *Heller* 9050 (NY, PA, US); Ruby Mts. near Blaine P. O., 3100 m. alt., Aug. 22, 1913, *Heller* 11108 (D, F, G, M,, NY, PA, UC, US); Jarbidge, 2300 m. alt., July 9, 1912, *Nelson & Macbride* 2004 (G, M, NY, RM, UAC, US); mouth of Thomas Creek and canyon, near LaMoille Creek, Ruby Mts., 2500 m. alt., July 16-19, 1938, *Rollins & Chambers* 2562 (G, UC, US); pasture, Golliher Mts., 18 mi. n.e. of San Jacinto, July 5, 1939, *Shipley* (UAC). EUREKA CO.: open hillsides, aspen belt, Windfall Canyon, Eureka, 2300 m. alt., June 16, 1936, *Train* (ARIZ, US). HUMBOLDT CO.: open mountain slopes, 2600-2800 m. alt., Buckskin Peak region, Santa Rosa Range, July 23, 1937, *Train* 514 (D, M, NY); dry slopes, Canyon Creek grade, west slope Santa Rosa Range, 2000 m. alt., July 21, 1937, *Train* 477 (ARIZ); Water Canyon, north end of Sonoma Range, July 4, 1937, *Train* 241 (CL-UC). WHITE PINE CO.: 7 mi. e. of Ely, 2400-3000 m. alt., Aug. 13, 1913, *Hitchcock* 1276 (US); northeast slope of Sherman Mt., south end of Ruby Mts., 3200 m. alt., Aug. 4, 1939, *Hitchcock & Martin* 5670 (CL-UC, NY, UC, UW); head of Lime Kiln Canyon, Nevada N. F., July 24, 1915, *Thompson* 14 (FS).

Oregon. HARNEY CO.: White Horse Mts., south of Old Fort Smith, Aug., 1901, *Griffith & Morris* 450 (NY, US); dry ground, upper Emigrant Creek, Aug. 1, 1912, *Peck* 4935 (D).

Utah. BOXELDER CO.: Brigham, July 20, 1880, *Jones* (P). CACHE CO.: Newton, June 19, 1917, *Jones* 507 (G); dry slopes, Pine Canyon, Wellsville Mts., June 18, 1932, *Maguire* 3154 (UAC); steep rocky slopes e. of High Creek Lake, 2700 m. alt., July 22, 1936, *Maguire, Hobson & Maguire* 14241 (PA, UAC, UC, UW). IRON CO.: 10 mi. e. of Cedar City, 2600 m. alt., July 29, 1933, *Graham* 8664 (M); spruce-fir forest, 3400 m. alt., 3 mi. n. of Cedar Breaks Lodge, Cedar Breaks Nat. Mon., Aug. 12, 1938, *Hitchcock, Rethke, & van Raadshooven* 4597 (CA, CO, D, IS, NY, P, RM, UAC, UC, UW, WS). MORGAN CO.: dry hills, Peterson Canyon, Peterson, 2800 m. alt., July 19, 1902, *Pammel & Blackwood* 3879 (IS). PIUTE CO.: mountains, Bullion Creek near Marysvale, July 23, 1905, *Rydberg & Carlton* 7124 (NY, RM, US). SALT LAKE CO.: Parley's Park, 2000 m. alt., June, 1869, *Watson* 605 (G, NY, US, type collection of *H. multicaulis* D. C. Eaton); Alta, Wasatch Mts., 3000 m. alt., Aug. 4, 1879, *Jones* 1177, 1178 (ARIZ, F, NY, P, RM, UAC, UO, US); Red Rock Canyon near Salt Lake City, June 11, 1905, *Rydberg* 6072 (NY, RM). SANPETE CO.: Ephraim, July 9, 1935, *Olsen* (CL-UC); .5 mi. w. of Experiment Sta., Manti N. F., 2900 m. alt., June 28, 1936, *Shafer* 19 (UAC). SUMMIT CO.: near Bear River, 820 m. alt., July 3, 1931, *Goodman* 1853 (G, M, NY, RM, US); Echo, Wasatch Mts., July 9, 1901, *Pammel*,

Johnson, Buchanan, & Lummis 1977 (IS). TOOELE CO.: head of North Oak Brush Canyon, 3100 m. alt., July 10, 1941, *Woolley* 16 (FS). UTAH CO.: top of Little Mountain, Wasatch Mts., June 30, 1897, *Swenson* 96 (D). WASHINGTON CO.: Right Fork Canyon, 2 mi. s.e. of Pine Valley Forest Camp, 2600 m. alt., July 15, 1942, *Gould* 1887 (ARIZ); rocky soil, Pine Valley Mts., 2000-2300 m. alt., May-Oct., 1898, *Purpus* 6214 (US).

WYOMING. ALBANY CO.: steep stony slopes, Centennial, July 26, 1900, *Nelson* 7713 (G, M, NY, P, RM, US). CARBON CO.: Encampment, 2400 m. alt., July 10, 1901, *Tweedy* 4054 (NY, US). FREMONT CO.: headwaters of Cliff Creek near Bondurant, 3000 m. alt., Aug. 9-18, 1900, *Curtis* (NY). LINCOLN CO.: gravelly knoll, 2300 m. alt., 2 mi. n. of Susie, July 2, 1938, *Hitchcock, Rethke, & van Raadshooven* 3886 (CO, D, G, UC, UW); shrubby hillsides e. of Afton, 2200 m. alt., June 30, 1923, *Payson & Armstrong* 3316 (CO, G, IS, M, P, PA, RM); Grand Canyon of the Snake River, 1800 m. alt., July 8, 1932, *Williams* 816 (CA, G, M, NY, RM, UAC). SUBLETTE CO.: aspen grove near lower end of New Fork Lakes, 2500 m. alt., July 21, 1925, *Payson & Payson* (G, M, PA, RM). TETON CO.: Jackson, 2000 m. alt., July 1, Aug. 10, 1913, *Maris* 154, 222 (FS); dry hillside in timber, Grand Teton N. P., 2300 m. alt., July 2, 1933, *Williams* 1209 (OSC, RM, UAC); slope of Mt. Moran, 2500-2800 m. alt., Jackson Hole, Grand Tetons, June 22-30, 1935, *Yuncker* 5418 (F). UINTA CO.: 16 mi. e. of Evanston, June 29, 1938, *Cutler* 2452 (CA, G, M).

YELLOWSTONE NATIONAL PARK: Cañon, July, 1904, *Oleson* 122 (IS).

4a. HELIANTHELLA UNIFLORA var. DOUGLASII (T. & G.) W. A. Weber

Helianthella Douglasii Torrey & Gray, Fl. N. Amer. 2: 334. 1842. *Helianthella uniflora* var. *Douglasii* W. A. Weber in Madroño 6: 186. 1948.

More hirsute in all its parts than the preceding; heads averaging larger, the involucre 2.0-2.5 cm. broad, the phyllaries more numerous, ciliate-hirsute, loose, the outermost rarely enlarged.

Type locality.—"Common on the subalpine range of the Blue Mountains," collected by Douglas, the type specimen at Kew.

Distribution.—Grasslands, northern Rocky Mountains, east slope of Cascade Range (exceptionally west of the crest, *e.g. Ownbey & Meyer* 2320, *Muenscher* 9026), and intermountain plateaus, from southern British Columbia to northern Idaho and central Oregon. Blooms from late May through July. Altitudinal range 350-2500 meters. (Map 3)

Canada.—BRITISH COLUMBIA: Spences Bridge, May 26, 1889, *Macoun* (G, NY); Whipsaw Creek, w. of Princeton, June 24, 1905, *Macoun* 46, 974 (NY); subalpine slopes near Lake Bootahnie, Marble Mts., 1600 m. alt., June 20-25, 1938, *Thompson & Thompson* 133 (M, NY, UW).

United States.—Idaho. CLEARWATER CO.: bank of Clearwater River 5 mi. s.e. of Orofino, May 28, 1944, *Hitchcock & Muhlick* 8444 (CA, UAC, UW, WS). ADAMS CO.: 20 mi. s. of New Meadows near road to Weiser, June 24, 1946, *Hitchcock & Muhlick* 13883 (RM, UAC, UC, UW); west fork Weiser River below Grouse Creek, Weiser N. F., 1200 m. alt., July 2, 1923, *Lommasson* 62 (FS). IDAHO CO.: Bear Creek R. S., 1060 m. alt., Selway N. F., T. 31 N., R. 13 E., S. 16, June 20, 1928, *Baker* (WS); bluff of Clearwater River opposite Kamiah, June 2, 1935, *Constance, Dimond, Rollins, & Worley* 1120 (G, M, WS); Graves Pt. L. O., T. 27 N., R. 1 W., June 24, 1940, *Davis* 2247 (PO, UAC, WS); Dry Diggins, Seven Devils Mts., T. 23 N., R. 2 W., 2400 m. alt., July 28, 1938, *Packard* 440 (WS). LATAH CO.: 5 mi. w. of Howard Creek along Camp Cougar road, June 17, 1936, *Dillon & Dillon* 631 (PO, WS); roadside, Moscow Mt., 1100 m. alt., July 7, 1943, *Murley* 1676 (IS, M); summit of Cedar Mt., 1600 m. alt., July 5, 1923, *Shaw* (WS). NEZ PERCES CO.: Lake Waha, 600-1100 m. alt., June 24, 1896, *Heller & Heller* 3292 (M, NY, UC, US); sandy soil,

valley of Big Potlatch River, June 6, 1892, *Sandberg, MacDougal, & Heller* 321 (CA, FC, G, NY, P, US). SHOSHONE CO.: near Santianne divide, west side, 1000 m. alt., Coeur d'Alene Mts., June 22, 1895, *Leiberg* 1017 (F, G, M, NY, P, RM, UC, US). WASHINGTON CO.: T. 16 N., R. 4 W., Sec. 21, Boise Meridian, 1300 m. alt., Weiser N. F., May 29, 1928, *Burr* 114 (FS); Manns Creek, 700 m. alt., July 8, 1899, *Jones* 6404 (M, P, US).

Oregon. BAKER CO.: Sumpter Valley watershed, 2500 m. alt., July 8, 1919, *Ferris & Duthie* 938 (D); Fish Lake, June 5, 1938, *Gustafson* (CL-UC, OSC). CLACKAMAS CO.: Cascade Mts., near Table Rock, Aug., 1900, *Howell* (UO). CROOK CO.: gulches of southern Blue Mts., 1300 m. alt., June 30, 1897, *Cusick* 1680 (D, G, M, UC, US, WS). DESCHUTES CO.: Bend, July 31, 1931, *Jones* (P). GRANT CO.: near Graylock, T. 16 S., R. 28 E., Sec. 32, 2300 m. alt., June 25, 1938, *Berghuis* 8 (FS); open hillside, entrance to Silvies River Valley, July 12, 1927, *Henderson* 8562 (CA, UO); Canyon City, John Day Valley, July 4, 1930, *Jones* 25067 (CA, D, M, P); Logan Valley, 1700 m. alt., Malheur N. F., July 6, 1928, *Renner* 1186 (FS). HARNEY CO.: open alpine slopes of King Mt., 2160 m. alt., July 12, 1935, *Thompson* 12020 (CA, CO, D, M, NY, P). UMATILLA CO.: Gibbon, June 4, 1910, *Heller* (CA). UNION CO.: moist bank 5 mi. n.w. of Elgin, July 16, 1944, *Peck* 22389 (CL-UC); stony loam, 1100 m. alt., T. 3 S., R. 41 E., Sec. 20, Whitman N. F., June 12, 1937, *Reid & Henderson* 433 (FS); near summit of Blue Mts., between Pendleton and La-Grande, June 14, 1928, *Thompson* 4733 (D, PA, US). WALLOWA CO.: open slope 28 mi. n. of Enterprise, June 23, 1934, *Peck* 18240 (D); Tepee Sprs., 1900 m. alt., Wallowa N. F., *Peterson* 270 (FS); rocky hillside, T. 3 N., R. 45 E., Sec. 19, 1800 m. alt., June 15, 1937, *Reid & Collins* (FS). WASCO CO.: yellow pine woods near Marion Point L. O., 1500 m. alt., Mt. Hood N. F., July 16, 1933, *Jones* 4039 (CA, CO, OSC, P, UW). WHEELER CO.: dry slope 7 mi. e. of Mitchell, July 9, 1921, *Peck* 10136 (CO, D, F, NY).

Washington. ASOTIN CO.: grassy meadows, 2 mi. n.e. of Anatone, May 30, 1936, *Meyer* 402 (M). CHELAN CO.: along Wenatchee River near suspension bridge above Chiwaukum, 590 m. alt., July 8, 1916, *Eggleston* 12293 (US); Peshastin, 360 m. alt., July 19, 1893, *Sandberg & Leiberg* 486 (UO, US, WS); wooded slopes on Tumwater Mt., above Leavenworth, 1000 m. alt., May 23, 1931, *Thompson* 6486 (D, G, M, OSC, PA, UW); rocky ground above Ingalls Creek, 1600 m. alt., June 19, 1935, *Thompson* 11724 (CA, CO, D, G, M, P, US, UW). KITTITAS CO.: Swauk River Valley, T. 17-18 N., R. 21 E., 750-1800 m. alt., May-Sept., 1913, *Sharples* 266 (CA, G, US) [leaves very broad, 3 at a node (G)]; sagebrush slopes, Virden, June 8, 1935, *Thompson* 11591 (CO, D, M, UW); mountainside n. of Ellensburg, June 12, 1898, *Whited* 663 (US). KLICKITAT CO.: grassy hillsides and plains, Mt. Adams, Aug. 1, 1883, *Suksdorf* 524 (F, PA, UC, US, WS); Gilmer Valley, June 22, 1918, *Suksdorf* 10077 (WS); Trout Lake Valley, June 20, 1890, *Suksdorf* 13098 (WS). OKANOGAN CO.: Bunker Mt., 1800 m. alt., July 29, 1916, *Eggleston* 13258 (US); 1 mi. w. of Salmon Meadows, July 4, 1931, *Fiker* 219 (WS); Slate Lake Trail from Twisp Valley, 17 mi. w. of Twisp, Aug. 12, 1942, *Hitchcock* 8101 (UW); dry, rocky slope, Harts Pass, 2000 m. alt., June 23, 1939, *Munescher & Muenscher* 15961 (G, UW); Angels Pass, 1600 m. alt., June 28, 1931, *Thompson* 7039 (D, G, M, PA, UC, UW). SPOKANE CO.: Spangle, June 19, 1884, *Suksdorf* 13076 (G, WS). WALLA WALLA CO.: Waitsburg, May 15, 1897, *Horner* B-280 (G, US). WHATCOM CO.: dry slope near Barron, Mt. Baker N. F., Aug. 11, 1937, *Munescher* 9026 (G); open brushy slopes down Slate Creek, w. of Harts Pass, July 29, 1940, *Ownbey & Meyer* 2320 (ARIZ, CA, G, IS, M, PO, OSC, UAC, US, UW, WS). WHITMAN CO.: Steptoe Butte, July 18, 1922, *Parker* 699 (WS); Pullman, June 30, 1893, *Piper* 1598 (F, G, NY, P, PA, RM, UW, WS); grassy slopes, Almota Canyon, May 30, 1922, *St. John* 3375 (WS); between Palouse and Colfax, May 22, 1941, *Weber* 2226 (CO, IS, M, UW, WS). YAKIMA CO.: east side, Mt. Adams, Aug. 24, 1908, *Suksdorf* 6350 (WS).

Helianthella uniflora and its variety *Douglasii* exhibit unusual local variation in leaf shape, a character which in most of the species is so stable and

distinctive as to be diagnostic. Plants with very broad, ovate leaves are found locally in the Wenatchee Mts., of Washington and in southern Montana. The repeated collection of such plants by different botanists suggests that entire populations in these areas may be affected. A pronounced tendency toward whorled leaves occurs in this broad-leaved form, and is exhibited by a few individuals of the normal type. In some collections the leaves taper to the base and apex and may even be distinctly petiolate. This variant is commonly confused with *H. quinquenervis*. The type specimen of *Helianthella lanceolata* (Nutt.) T. & G. is such an individual.

Large series of specimens are needed from southern and southwestern Montana, where puzzling intermediates occur which appear to connect *H. uniflora* with its variety *Douglasii*. Although most specimens from this region are typical *uniflora*, certain individuals have the larger heads and ciliate phyllaries of the variety (*Hitchcock & Muhlick* 15251). Both types of individuals have been observed in a series belonging to a single collection number.

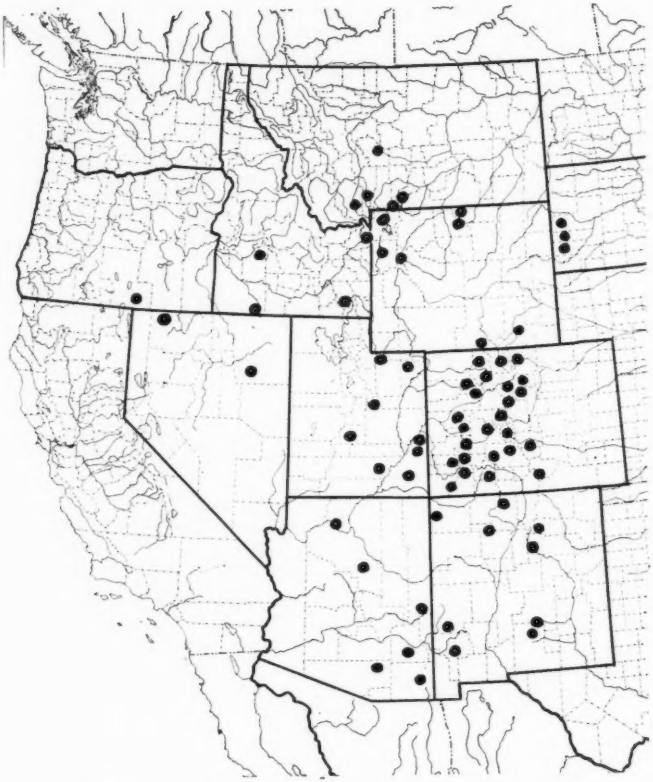
5. HELIANTHELLA QUINQUENERVIS (Hooker) A. Gray

Helianthus quinquenervis Hooker in London Jour. Bot. 6: 247. 1847. *Helianthella quinquenervis* A. Gray in Proc. Amer. Acad. 19: 10. 1883. *Helianthella quinquenervis* var. *arizonica* Gray, Syn. Fl. 1 (2): 284. 1884. *Helianthella majuscula* Greene in Leafl. Bot. Obs. & Crit. 1: 148. 1905.

Stem stout, erect, 5-15 dm. tall, sparsely hirsute or glabrate; leaves leathery, about four opposite cauline pairs, the middle largest, ovate-lanceolate to elliptic-lanceolate, up to 50 cm. long, acuminate at each end, tapering to a prominent petiole, two pairs of lateral veins usually prominent; head solitary, long-peduncled, nodding, a few reduced lateral heads often present; involucre 4-5 cm. broad, 2 cm. high; phyllaries broadly ovate-lanceolate, acute or acuminate, ciliate-margined, blackening on drying; receptacular paleae soft and scarious; ray-flowers bright yellow, 2.5-3.0 cm. long; disk-flowers yellow; cypsela 8-10 mm. long, ciliate-margined, appressed-pubescent on the faces, blackish-brown; pappus of two slender awns one-half the length of the cypsela; intermediate squamellae well-developed.

Type locality.—"Stony ridges of the Upper Platte, with *Balsamorhiza helianthoides;* rare (n. 33)," collected by Geyer. The collector's journal (Geyer, 1845-1846, pp. 39-40) contains a description of the type station, as follows: "once again, a 3 days journey through syenitic and pseudobasaltic confused hills and mountains, we are at last out of this rich group, and have arrived at Rock Independence. At the crossing-place of the northern arm of the Platte, the hills are already about 1,000 feet high, and showed at that time, July 15, snow in the high defiles . . . Here already occurs . . . Heliantheae 33 . . ." The type locality, therefore, was near the crossing of the Sweetwater River, which might be called the "northern arm of the Platte," in the vicinity of Independence Rock and near Devil's Gate, in what is now southwestern Natrona County, Wyoming (C. L. Porter, in correspondence with the author).

Distribution.—Mountain meadows, frequently in wet or boggy places, aspen and lodgepole pine forests, and (in the southern portion of the range)



Map 4.—Distribution of *Helianthella quinquenervis* (see also Map 2)

ponderosa pine forests, Rocky Mountains from southern Idaho, southern Montana, and the Black Hills of South Dakota, through the mountainous portions of Colorado, Utah, Wyoming, New Mexico, and Arizona, to Chihuahua and Nuevo Leon, Mexico. One collection from Lake County, Oregon. The species probably occurs in the Big Bend region of Texas and through Coahuila, but collections are lacking. Altitudinal range 1600 (in the north) to 4000 (in the south) meters. Blooms in July and August. (Map 4)

United States.—Arizona. APACHE Co.: 6 mi. s. of Hannagan Meadows, White Mts., 3100 m. alt., Aug. 11, 1935, *Kearney & Peebles* 12275 (US); McNary, 2800 m. alt., July 27, 1936, *Fisher* 36156 (US). COCHISE Co.: open slopes, Carr Peak, July 22, 1909, *Goodding* 265 (ARIZ, G, NY, RM); rolling andesitic pineland, Barfoot Park, 2600 m. alt., Oct. 3, 1906, *Blumer* 1442 (ARIZ, D, F, G, IS, M, NMX, NY, RM,

US). COCONINO Co.: 1 mi. n. of North Gate, Grand Canyon Nat. Park, 2900 m. alt., July 23, 1941, *Munz* 16983 (P, WS); grassy openings under ponderosa pine, Fort Valley Exp. Sta. Hdqs., 9 mi. e. of Flagstaff, July 18, 1946, *Parker* 5944 (CO, UAC); 2300 m. alt., Bill Williams Mt., July 22, 1898, *MacDougal* 312 (F, G, IS, NY, PA, UC, US). GRAHAM Co.: near summit, Graham Mts., Sept. 7-13, 1914, *Thornber & Shreve* 7758 (ARIZ); Shannon Camp, Pinaleño Mts., 2900 m. alt., Sept. 3, 1944, *Darrow, Phillips, & Pultz* 1074 (ARIZ). PIMA Co.: Mt. Lemmon, Santa Catalina Mts., Aug. 5, 1908, *Livingston & Thornber* (ARIZ, NY).

Colorado. BOULDER Co.: Gillham's Gulch, Ward, 3000 m. alt., July 20, 1921, *Schmoll* 342 (CO); Lake Eldora, 3100 m. alt., Aug. 1, 1918, *Clokey* 3135 (CA, CL-UC, D, P, RM, US). CHAFFEE Co.: Mt. Harvard, 1896, *Clements* 56 (NY). DELTA Co.: LeRoux Park, July 19, 1892, *Cowen* 714 (FC). FREMONT Co.: Wet Mountain Valley, Aug., 1873, *Brandegee* 712 (M, PA, UC). GARFIELD Co.: Little Trappers Lake, 3160 m. alt., Aug. 3, 1933, *Hermann* 5644 (G, M, NY). GILPIN Co.: hillside, Tolland, 2900 m. alt., July 19, 1917, *Clokey* 2846 (CA, CL-UC, F, M). GRAND Co.: Fraser, Aug. 3, 1888, *Holway* (IS); Berthoud Pass, 3600 m. alt., July, 1903, *Tweedy* 5860 (NY, RM). GUNNISON Co.: vicinity of Mt. Carbon, 3000 m. alt., June 29, 1910, *Eggleston* 5781 (US); Irwin, Elk Mts., Aug. 3, 1889, *Eastwood* (CO) [upper 2 sets of leaves in whorls of 3]; hills n.e. of Gothic, 8 mi. n. of Crested Butte, July 29, 1937, *Wherry* 3722 (CA). HUERFANO Co.: meadow near Cuchara Camps, July 5, 1934, *Stigall* (CO). JACKSON Co.: boggy ground in open pine woods, North Park near Teller, 2600 m. alt., July 31, 1884, *Sheldon* 151 (F, M, NY, PA). LAKE Co.: Leadville, 2700 m. alt., Aug. 1, 1912, *Stewart* 43 (FS). LA PLATA Co.: Durango-Silverton Hwy., Durango, July 16, 1924, *Schmoll* 1527 (CO, RM); Elbert Creek, T. 38 N., R. 9 W., Sec. 5, 3000 m. alt., San Juan N. F., July 3, 1934, *Loughridge* 262 (FS). LARIMER Co.: Rist Canyon, July 15, 1909, *Smith* (FC); Chambers Lake, Aug. 22, 1908, *Osterhout* 3854 (RM); Cameron Pass, Aug. 2, 1913, *Osterhout* 7921 (RM). MESA Co.: 3 mi. above Lake Resort, Mesa Grande, July 17, 1935, *Maguire* 12473 (UAC); aspen woodland on eastern slope, 27 mi. above Delta, July 17, 1935, *Maguire* 12479 (UAC). MINERAL Co.: summit, Wolf Creek Pass, 3600 m. alt., July 28, 1928, *Wolf* 3029 (CA, D, G). MONTEZUMA Co.: Chicken Creek, w. of Mt. Hesperus, 2600 m. alt., July 7, 1898, *Baker, Earle, & Tracy* 645 *in part* (G, NMX, RM, UC). MONTROSE Co.: Cerro Summit, 2600 m. alt., July 12, 1901, *Baker* 415 (G, M, NY, P, RM, UC); Tabeguache Basin, 2600 m. alt., July 26, 1914, *Payson* 525 (G, M, RM). OURAY Co.: Mt. Abram, Ouray, July 27, 1897, *Shear* 4135, 4140 (NY). RIO BLANCO Co.: mountain parks, T. 2 S., R. 91 W., Sec. 9, 2900 m. alt., July 15, 1932, *Ware* 261 (FS). ROUTT Co.: Steamboat Springs, July 14, 1902, *Osterhout* 2689 (RM); Little Columbine Lake, Aug. 12, 1938, *Ramaley & Ewan* 16692 (CO). SAGUACHE Co.: Marshall Pass, 3300 m. alt., July 19, 1901, *Baker* 475 (G, M, NY, P, RM, UC, US); Villa Grove, July 23, 1896, *Shear* 5098 (NY). SAN JUAN Co.: Ironton, July 21-31, 1899, *Curtis* (NY). SAN MIGUEL Co.: Telluride, 3600 m. alt., Aug., 1894, *Tweedy* 326 (US). SUMMIT Co.: Breckenridge, 3200 m. alt., Aug., 1901, *Mackenzie* 89 (M, NY, RM). COUNTY UNCERTAIN: South Park, July, 1873, *Wolf & Rothrock* 546 (F, NY, PA, US).

Idaho. BANNOCK Co.: Johnson Creek, Caribou N. F., 2400 m. alt., July 27, 1914, *Favre* 258 (FS). ELMORE Co.: Campo Creek, 1800 m. alt., Boise N. F., July 29, 1929, *Saling* 22 (FS). FREMONT Co.: lodgepole pine forest along road to Squirrel Meadows, e. of Ashton along Idaho-Wyoming border, 2200 m. alt., July 16, 1939, *Cronquist* 1726 (M, PO, UAC). OWYHEE Co.: Owyhee Mts., July 7, 1892, *Mulford* (G, M, NY).

Montana. GALLATIN Co.: moist meadowland, Bridger Mts., 1 mi. s. of Brackett Cr., 2500 m. alt., July 18, 1945, *Hitchcock & Muhlick* 12459 (OSC, RM, UAC, UW, WS). MADISON Co.: dry hills along west Hammond Cr., 13 mi. e. of Ennis, July 23, 1947, *Hitchcock* 16731 (UW). MEAGHER Co.: 2000 m. alt., Little Belt Mts., 9 mi. from Barker, Aug. 19, 1896, *Flodman* 872 (M, NY, US). PARK Co.: 2 mi. s. of Cooke City, Aug. 13, 1945, *Hitchcock & Muhlick* 13602 (CO, UW, WS). STILL-

WATER Co.: just s. of Independence, 2600 m. alt., Aug. 8, 1945, *Hitchcock & Muhlick* 13461 (OSC, RM, UAC, UW, WS).

Nevada. ELKO Co.: *Pinus flexilis* woodland, Le Moille Canyon, Ruby Mts., 3000 m. alt., Aug. 19, 1943, *Maguire & Holmgren* 22671 (G, NY, UAC). HUMBOLDT Co.: head of Alder Creek, Pine Forest Mts., 2600 m. alt., July, 1909, *Taylor & Richardson* 1 (UC).

New Mexico. CATRON Co.: Mogollon Mts., on or near west fork Gila River, 3600 m. alt., Aug. 15, 1903, *Metcalfe* 513 (ARIZ, CL-UC, G, M, NY, RM, US). GRANT Co.: pine timber, Sawyers Peak, 3160 m. alt., south end of Black Range, Sept. 30, 1904, *Metcalfe* 1435 (CL-UC, F, G, M, NY, P, US, isotypes of *H. majuscula* Greene). LINCOLN Co.: Ruidoso, 2700 m. alt., July 9, 1938, *Fisher* 38175 (F) [upper stem leaves sessile, clasping]. MORA Co.: Pecos Baldy, 3600 m. alt., July 30, 1903, *Bailey* 565 (US). OTERO Co.: summit of Sierra Blanca Peak, Mescalero Apache Reservation, 4,000 m. alt., July 22, 1931, *Huber* (PA); Cloudcroft, July 31, 1889, *Wooton* (US); Cold Spring Canyon, Sacramento Mts., Aug. 17, 1899, *Wooton* (US). RIO ARRIBA Co.: Chama, 2380-2850 m. alt., July 10, 1911, *Standley* 6775 (US). SANDOVAL Co.: yellow pine forest s.e. of Cuba, 2700 m. alt., Aug. 1, 1915, *Read* 27 (US). SAN JUAN Co.: Navajo Indian Res., Tunitcha Mts., Aug. 8, 1911, *Standley* 7555 (US). SAN MIGUEL Co.: Ponchuelo Creek, 2800 m. alt., July 9, 1908, *Standley* 4266 (F, G, M, NMX, NY, US); Upper Round Mt., above Cowles, July 26, 1931, *Castetter* 766 (RM).

Oregon. LAKE Co.: Warner Range, 1650 m. alt, July 26, 1896, *Coville & Leiberg* 52 (UO, US).

South Dakota. CUSTER Co.: Sips Springs, limestone district w. of Custer, 2000 m. alt., July 29, 1892, *Rydberg* 807 (G, NY, US). LAWRENCE Co.: open woods, Dumont, Aug. 28, 1924, *Over* 16233 (RM, US); 10 mi. w. of Lead, July 6, 1925, *McIntosh* 698 (RM). PENNINGTON Co.: wooded slopes, aspen-yellow pine, limestone district 12 mi. w. of Deerfield, July 22, 1927, *Hayward* 2320, 2743 (F, RM).

Utah. CARBON Co.: meadow-pasture n.w. of Willow Springs, 10 mi. e. of Sunnyside, 3200 m. alt., July 10, 1935, *Graham* 9540 (F, UAC). GARFIELD Co.: Bromide Pass, Henry Mts., July 27, 1894, *Jones* 5686 (NY, UC, US). GRAND Co.: rocky, grassy slopes, La Sal Mts., July 21, 1924, *Payson & Payson* 3939 (D, G, RM, UC); gravelly s.w. slopes of Mt. Hobbs, 3400 m. alt., July 22, 1933, *Maguire, Richards, Maguire & Hammond* 18007 (UAC, UC, UW). SAN JUAN Co.: La Sal Mts., near Mt. Peale, 3300-3700 m. alt., July 17, 1911, *Rydberg & Garrett* 9004 (NY, RM, UC, US); Abajo Mts., near Spring Creek, 2700-3000 m. alt., Aug. 17-20, 1911, *Rydberg & Garrett* 9716 (NY). SEVIER Co.: Mt. Hilgard, Wasatch Mts., 3100 m. alt., Aug. 1, 1914, *Eggleston* 10348 (US). SUMMIT Co.: Black Forks R. S., Wasatch N. F., 2900 m. alt., Aug. 15, 1922, *McDonald* 20 (FS); open lodgepole forest, upper Stillwater Fork, LaMotte Peak area, July 26, 1926, *Payson & Payson* 5107 (RM). UINTAH Co.: in sagebrush, s.e. slope of Mosby Mt., 2600 m. alt., July 3, 1933, *Graham* 8341 (F, G, M).

Wyoming. ALBANY Co.: Chug Creek, June 29, 1900, *Nelson* 7301 (G, IS, M, NY, P, US); Crow Creek, July 8, 1903, *Nelson* 8903 (CO, G, M, NY, RM, US). BIG HORN Co.: Brokenback Creek, T. 49 N., R. 87 W., 2500 m. alt., Bighorn N. F., July 2, 1932, *Post* 288 (FS); slopes of Little Bald Mt., 3000 m. alt., July 6, 1936, *Williams & Williams* 3254. (G, M, NY, RM, UW, WS). CARBON Co.: 3300-3600 m. alt., July 20, 1901, *Tweedy* 4055 (NY, US). FREMONT Co.: Warm Spring Creek, Aug. 10, 1894, *Nelson* 803 (M, US); Union Pass, Aug. 10, 1894, *Nelson* 803 (2899) (G, NY, RM). SHERIDAN Co.: rich meadows, Big Horn Mts., 2600 m. alt., Aug., 1899, *Tweedy* 2056 (NY); Little Goose Canyon, July 5, 1909, *Willits* 224 (RM). TETON Co.: meadow, Moran, July 21, 1932, *Rose* 32430 (CA); summit of Teton Pass, Aug. 16, 1937, *Cronquist* 827-37 (UAC, UC).

YELLOWSTONE NAT. PARK: Turbin Lake, 3100 m. alt., Aug. 15, 1928, *Smith* 66 (WS); Snake River, Aug. 12, 1899, *Nelson & Nelson* 6409 (G, M, NY, RM, US).

MEXICO.—CHIHUAHUA: in shallow pond, Chuhuichupa, Aug.-Sept., 1936, *LeSueur* 1004 (F); 60 mi. s. of Guadelupe y Calvo, 2500-2800 m. alt., Aug. 20, 1898, *Nelson* 4808 (G, US); moist edge of prairie near San Juanito, Dtr. de Bocoyna, 2600 m. alt., July 26, 1937, *Shreve* 8033 (ARIZ, F, US). NUEVO LEON: abundant over small areas in upper pine wood, peak of Cerro Potosí, Municipio de Galeana. July 21, 1935, *Mueller* 2277 (F, G).

Helianthella quinquenervis is easily recognized by its large, usually 5-nerved leaves which are acuminate at each end, its broad, prominently ciliate phyllaries which usually turn black in drying, and its large head which is turned with the axis at right angles to the stem, a characteristic which it shares with its close relative, *H. Parryi*. In all other species the head is erect.

In dry habitats, particularly through the southern part of the range, this species becomes somewhat dwarfed and more strongly hirsute-pubescent. Greene's *H. majuscula* represents variants of this type.

6. HELIANTHELLA PARRYI A. Gray

Helianthella Parryi A. Gray in Proc. Acad. Sci. Phila. 1863: 65. 1864.

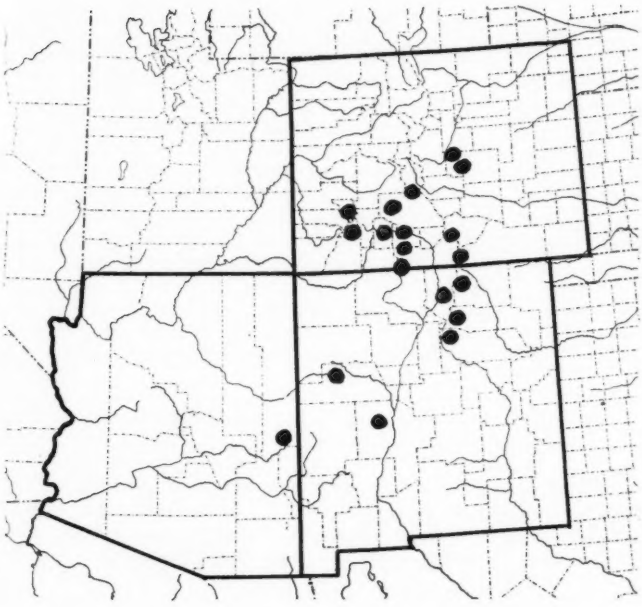
Stem 2-5 dm. tall, arising from a slender caudex; foliage appressed-hirsutulous, becoming glabrate or merely ciliate in age; resin droplets minute or absent; basal leaves 3-nerved, spatulate, acute, tapering to long petioles; cauline leaves greatly reduced, subsessile, arranged in one or two opposite pairs or rarely whorls of three leaves, or a few of the uppermost alternate; heads solitary or few, the axillary heads often smaller or abortive; involucre 1.5-2.0 cm. broad, 1 cm. high, nodding; phyllaries subequal, lanceolate, acuminate, conspicuously ciliate; receptacular paleae thin and scarious; disk-corollas about 5 mm. long, pale yellow; ray-corollas 8-10, pale yellow when fresh (deep yellow in dried specimens), 25-30 mm. long, 5-7 mm. wide; cypsela oblanceolate, emarginate, black and lustrous, 7-8 mm. long excluding the very short awns and intermediate squamellae; margins and faces densely appressed-pilose.

Type locality.—"Foot of Pikes Peak [El Paso County,] Colorado." Collected by Parry, 1862.

Distribution.—Upper montane forests (under *Pinus ponderosa* at the type locality) to the timberline (in the southern part of the range), in the Rampart, Sangre de Cristo, Culebra, and San Juan ranges of southern Colorado and northern New Mexico, the Zuni Mts. of western New Mexico, and the White Mts. of eastern Arizona. Blooms from late June through early August. Altitudinal range 2400 to 3600 meters. (Map 5)

Arizona. APACHE CO.: Atoscacita Spring, Apache N. F., 2570 m. alt., Aug. 19, 1920, *Eggleston* 17051 (US); White Mts., Aug. 6-15, 1903, *Griffiths* 5266 (US).

Colorado. CHAFFEE-SAGUACHE COS.: Marshall Pass, 1896, *Clements* 151 (NY). CONEJOS CO.: Alamosa River, 3100 m. alt., Rio Grande N. F., July 3, 1939, *Gierisch* 1043 (FS); Conejos Canyon, 3300 m. alt., July 24, 1936, *Ramaley* 15658 (CO); near Cumbres Pass, July 24, 1936, *Ramaley* 15685 (CO); near Jasper, July 26, 1938, *Ramaley* 16647 (CO). COSTILLA-HUERFANO COS.: La Veta Pass, 1877, *Hooker & Gray* (G). COSTILLA CO.: east side of La Veta Pass, 3000 m. alt., July 20, 1938, *Hitchcock, Rethke & van Raadshooven* 4161 (CO, UW). EL PASO CO.: Table Rock, July 14, 1891, *Breninger* 1484 (FC); Ruxton Dell, 2950 m. alt., July 18, 1901, *Clements & Clements* 187 (D, G, IS, M, NY, US); Ute Pass road to Petrified Stump, Aug. 3,



Map 5.—Distribution of *Helianthella Parryi*

1884, *Letterman* (G, M); foot of Pikes Peak, alpine and subalpine, 1862, *Parry* (G type, M, NY, PAR, US isotypes); Barr Trail, south slope, Pikes Peak, 3300 m. alt., July 16, 1923, *Penfound* 133 (CO); gravelly slopes, Green Mountain Falls, 2800 m. alt., Aug. 2, 1892, *Sheldon* 5834 (NY). LAS ANIMAS CO.: Stonewall, Aug., 1917, *Beckwith* 296 (NY). OURAY CO.: Ouray, June 24, 1898, *Bethel* (FC). MINERAL CO.: s. side of Wagon Wheel Gap, 3300 m. alt., July 19, 1938, *Hitchcock, Rethke & van Raadshooven* 4137 (CA, CO, D, G, UW). RIO GRANDE CO.: east fork, Frisco Creek, Rio Grande N. F., July 6, 1939, *Gierisch* 1055 (FS); hillside near South Fork, 2700 m. alt., July 5, 1914, *McNair* 112 (FS); Rock Creek, s.w. of Monte Vista, 3000 m. alt., Sept. 9, 1935, *Ramaley* 15267 (CO). SAGUACHE CO.: Spanish Creek, Cochetopa N. F., 2730 m. alt., July 22-29, 1910, *Eggleston* 5994 (US); dry hillsides, forest openings, Cochetopa Pass, 3300 m. alt., July 14, 1939, *Ramaley & Gambill* 16917 (CO); aspen forest, 3150 m. alt., Saguache Creek Canyon, July 22, 1936, *Ramaley* 15555 (CO, RM). SAN JUAN CO.: Silverton, July, 1889, *Eastwood* (CO, US). TELLER CO.: Ute Pass, July 22, 1872, *Porter* (G, M, PA); Woodland Park R. S., Pike N. F., 2800 m. alt., July 12, 1928, *Lister* 94 (FS); near Florissant, 2400 m. alt., Aug. 1-8, 1905, *Ramaley* 1330 (CO).

New Mexico. COLFAX CO.: Cimarron Canyon, 2600 m. alt., Aug. 11, 1923, *Eggleston* 19004 (US); Ute Park, 2200-2900 m. alt., Aug. 20, 1916, *Standley* 13379 (US); Baldy Peak, above timberline, 3600 m. alt., Sept. 4, 1916, *Standley* 14362 (US). MORA CO.: Mora, Aug. 11, 1910, *Wooton* (US). SAN MIGUEL CO.: mountains back of Rociada, Aug., 1905, *Dandelin* (G); Harveys Upper Ranch, 3200 m. alt., Aug. 1,

1908, *Standley* 4684 (G, M, NMX, NY, US). SOCORRO CO.: Litle Baldy Peak, Magdalena Mts., Aug. 24, 1903, *Diehl* (P). TAOS CO.: Apache Peak, Carson Forest, 3000 m. alt., Aug. 22, 1923, *Eggleston* 19177 (US). VALENCIA CO.: mountains w. of Grants Station, Aug. 2, 1892, *Wooton* (US).

7. HELIANTHELLA CALIFORNICA A. Gray

Helianthella californica A. Gray *apud* Torrey in Pacific Railroad Rep't. 4: 103. 1856.

Stems and caudices slender, 1.5-6.0 dm. tall; foliage minutely appressed-hirsutulous, becoming glabrate or scaberulous in age; leaves oblong-lanceolate, 5-26 cm. long, tapering to elongate petioles, the lowermost cauline leaves opposite; heads usually solitary, on long peduncles; involucre 1.5-2.5 cm. broad; phyllaries lanceolate, densely pubescent to ciliate or glabrate; disk-corollas yellow; ray-corollas bright yellow, 1.5-2.0 cm. long, not greatly exceeding the involucre; cypsela cuneate-obovate, strongly compressed, 6-10 mm. long, dull brown, glabrous, deeply emarginate at the summit; pappus none.

Type locality.—"Napa Valley, California, on hillsides." Collected by Dr. J. M. Bigelow, 1853, 1854.

Distribution.—San Francisco Bay area and adjacent Napa Valley, north to Mendocino and Glenn counties, California. Altitudinal range, sea level to 1000 m. alt. Blooms in May and June. The species proper is replaced in the Sierra Nevada by the variety *nevadensis*. (see Map 6)

California. ALAMEDA CO.: Cedar (Cypress) Mt., 14 mi. from Livermore, May, 1903, *Elmer* 4488 (ARIZ, CA, D, M, NY, P, UO, US, WS). GLENN CO.: 11 mi. n.e. of Alder Sprs., 400 m. alt., May 19, 1949, *Munz* 13336 (CO). LAKE CO.: Mt. Konocti, 1000 m. alt., May 27, 1929, *Blankinship* (M); Allen Sprs., June, 1882, *Cleveland* (D, G, UC); s. of Kelseyville on road to Adams Sprs., May 18, 1938, *Eastwood & Howell* 5736 (CA, UW). MENDOCINO CO.: Ukiah, June 13, 1913, *Eastwood* 3341 (G); Lakeport-Hopland road near crest of road grade on mountain pass, May 4, 1940, *Gould* 1031 (NY); shaded slope at Carl Purdy's place near Ukiah, Mayacama Mts., June 15, 1931, *Howell* 6704 (CA, D). NAPA CO.: Napa Valley, 1853-54, *Bigelow* (G type, NY isotype); Wooden Valley grade, July 4, 1937, *Howell* 13057 (CA, CL-UC). SAN MATEO CO.: near Searsville, May 11, 1895, *Applegate* 264 (D); Jasper Ridge, Santa Cruz Mt. peninsula, May 9, 1911, *McMurphy* (CO, P, UW). SANTA CLARA CO.: open wooded slopes above Isabel Creek, Mt. Hamilton range, May, 1923, *Bacigalupi* (D, P); road to Madrone Springs, June 5, 1937, *Eastwood & Howell* 4533 (CA, M); Smith Creek, foot of Mt. Hamilton, May 10, 1907, *Heller* 8522 (D, F, G, IS, M, NY, PA, US); n.e. ridge of Copernicus Peak, Mt. Hamilton, 1380 m. alt., under *Pinus Sabiniana*, May 1, 1934, *Sharsmith* 1035 (UC). SOLANO CO.: Vaca Mts., May, 1893, *Jepson* (UC). SONOMA CO.: Altruria, April 7, 1900, *Eastwood* (G, UC, US); Mt. Hood, Mar. 31, 1902, *Heller & Brown* 5192 (D, F, G, M, NY, PA, US, UW); Rincon Ridge, 4 mi. e. of Santa Rosa, 130 m. alt., May 22, 1941, *Rose* 41246 (CL-UC, G, NY).

7a. HELIANTHELLA CALIFORNICA var. NEVADENSIS (Greene) Jepson

Helianthella nevadensis Greene in Bull. Calif. Acad. Sci. 1 (3): 89. 1885. *Helianthella californica* var. *nevadensis* Jepson, Man. Fl. Pl. Calif. 1081. 1925.

Consistently differing from the species proper only as to the cypselae,

which always bear two short, persistent awns and usually several low intermediate squamellae.

Type locality.—Greene applied the name *Helianthella nevadensis* to "*H. californica* Gray, of Bot. Cal. and Syn. Fl. as to the plant of the Sierra only." Unfortunately, Dr. Gray did not cite a specimen from the Sierra Nevada in either of the above works. Furthermore, none of the specimens now in the Herbarium Greeneanum were collected at a date early enough to have been available to Greene at the time of publication of *H. nevadensis*. Therefore, the following collection is hereby designated as lectotype: *E. B. Copeland* 695, in chaparral at "The Summit," Jonesville, Butte Co., California, 2150 m. alt., June 22, 1931 (UC).

Distribution.—Meadows, open forests, and chaparral, in an area roughly coinciding with the *Pinus ponderosa* belt, Sierra Nevada from southern Oregon southward to Kern County, California, Washoe County, Nevada, and

Figs. 1-3.—1. *Helianthella Parryi.* Diakinesis in microsporocyte. ×1200. 2. *Helianthella californica.* Diakinesis in microsporocyte. ×1300. 3. *Helianthella castanea.* Metaphase II in meiotic division of microsporocyte. ×1650.

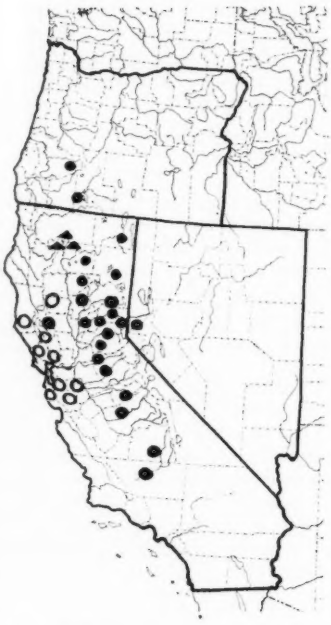
west of the Sacramento Valley to Lake County, California. Altitudinal range 200 to 2300 meters.

California. AMADOR CO.: Agric. Sta., 660 m. alt., Aug., 1891, *Hansen* 167 (CA, D, US). BUTTE CO.: in chaparral at "The Summit," Jonesville, 2150 m. alt., June 22, 1931, *Copeland* 695 (ARIZ, CA, D, F, G, M, NY, P, R, RM, UAC, UC, UO); ridge above Enterprise, 660 m. alt., in red clay soil, north slope near lower limit of yellow pine belt, May 25, 1915, *Heller* 11897 CA, CL-UC, CO, D, F, G, M, OSC, US). CALAVERAS CO.: shaded woods, Murphy's Camp, May 18-30, 1895, *Burtt-Davy* 1508 (UC); Calaveras R. S., Stanislaus N. F., 1000 m. alt., May 26-June 8, 1913, *Eggleston* 9186 (US). ELDORADO CO.: grassy places, Inst. Forest Genetics Arboretum, 3 mi. e. of Placerville, 900 m. alt., April 28, 1943, *Robbins* 1042 (UC, WS). KERN CO.: Mt. Breckinridge, June 14, 1905, *Grinnell* 271 (US); north fork Kern River near Kernville, June 7-15, 1888, *Palmer* 106B (US). LAKE CO.: Smith Mt., June 24, 1891, *Brandegee* (US). LASSEN CO.: Susanville, July 1, 1892, *Brandegee* (UC); near Blacks Lake, July 11, 1934, *Howell* 12561 (CA, D); Susanville, 1400 m. alt., June 25, 1897, *Jones* (NMX). MADERA CO.: North Fork, April 26, 1934, *Bacigalupi* 2293 (CO, D, UC). MARIPOSA CO.: grassy meadows, Wawona, 1300 m. alt., June 5, 1924, *Howell* 378 (CA); 1.5 mi. from Midway on road to Wawona, 1260 m. alt., June 29, 1933, *Wolf* 5102 (CO, UW). MODOC CO.: red soil, pine timber, June 20, 1893, *Baker* (NY, P, UC). NEVADA CO.: Nevada City, Jnue 20-22, 1912, *Eastwood* 535 (CA); Cisco-Red Mt. trail, Tahoe Forest, 1900-2300 m. alt., June 4, 1928, *Eggleston* 22191 (US); along Coldstream 3 mi. above Truckee, July 23, 1903, *Heller* 7006 (CO, D, G, IS, M, NY, P, PA, RM, UC, US); under yellow pines 1 mi. w. of Donner Summit, 2000 m. alt., July 23, 1939, *Maguire* 17221 (G, PA, UAC). PLACER CO.: Cascade Lakes, T. 17 N., R. 14 E., Sec. 32, 2200 m. alt., Tahoe N. F., July 4, 1934, *Bolt* 5845 (FS); Meier Ranch, ca. 6 mi. n. of Colfax, 800 m. alt., pine-oak ass'n., May 14, 1940, *Hitchcock* 6392 (CL-UC, NY, P, UAC, UW). PLUMAS CO.: Gold Lake region, July 11, 1927, *Bacigalupi* 1719 (NY, P); Forest Lodge, Greenville, June 13, 1927, *Eastwood* 14555 (CA); Prattville, 1500 m. alt., July 5, 1897, *Jones* (CO, P, UAC); partial shade on dry mountain slope, spruce forest, 1220 m. alt., Quincy, July 3-5, 1932, *Keck* 1651 (D); mountains n. of Sierra Valley, 2000 m. alt., T. 23 N., R. 15 E., Sec. 1, Aug. 9, 1934, *Hanks* 24 (FS); Onion Valley, 2000 m. alt., Plumas N. F., July 5, 1934, *Swift* 92 (FS). SHASTA CO.: dry hillside, Trinity Ridge, June 14, 1896, *Blasdale* (UC); near Pit River Ferry, 200-300 m. alt., May 15, 28, 1897, *Brown* 246 (F, M, NY, PA, US). SIERRA CO.: granitic, rocky soil, *Pinus ponderosa, Pseudotsuga taxifolia, Quercus Kelloggii, Q. chrysolepis* ass'n., junction of North and South Forks of North Fork of Yuba River, Sierra City, 1500 m. alt., June 9, 1938, *Constance* 2301 (G, M, NY, RM, UAC, UC, UW, WS); Salmon Lake, 2100 m. alt., July 12, 1921, *Evans* (F); dry, open flats, Gold Lake, 2100 m. alt., July 15, 1934, *Rose* 34366 (CA, D, F, NY, P, UW). TEHAMA CO.: Mill Creek Canyon, 1600 m. alt., near Morgan, July 1, 2, 1903, *Hall & Babcock* 4411 (UC). TULARE CO.: Pine Flat, near Cal. Hot Sprs., June 18, 1917, *Moxley* 543 (UC). YUBA CO.: near Dobbins, 800 m. alt., Plumas N. F., May 10, 1932, *Swift* 55 (FS).

Nevada. WASHOE CO.: Reno, *Hillman* (CO, P); Incline, Aug. 1, 1928, *Smith* (UAC).

Oregon. DOUGLAS CO.: grassy slopes, Umpqua Divide, head of Elk Creek, 1500 m. alt., July 2, 1899, *Leiberg* 4191 (UO, US). KLAMATH CO.: east side, Johnson Prairie, in dry yellow pine woods, 1300 m. alt., June 13, 1898, *Applegate* 2439 (D, NY, US).

Since Jepson did not discuss his reasons for reducing *H. nevadensis* to varietal status under *H. californica*, an evaluation of the criteria used by Greene to distinguish the two forms is in order. Greene's comparison is given below in tabular form.



H. californica

Almost glabrous
Stems branching, 2 feet high
Leaves all opposite except occasionally a single one a little below the head
Akenes cuneate-obovate, slightly obcordate, glabrous, with traces of wings above, but wholly destitute of pappus
Terminal areola prominently elevated

H. nevadensis

Minutely scabrous-puberulent
Stems simple, bearing at summit about 3 short-peduncled heads
The upper [leaves] usually alternate
Akenes obovate-oblong, not cuneate at base, glabrous except the ciliolate margins of the imperfect wings, less obcordate; pappus of 2 short, firmly persistent awns, and numerous intermediate, equally persistent squamellae
Terminal areola depressed

Map 6.—Distribution of *Helianthella californica* (open circles), *H. californica* var. *nevadensis* (dots), and *H. californica* var. *shastensis* (triangles).

The following comments regarding this comparison are made on the basis of study of large series of specimens.

The separation of *californica* and *nevadensis* on the basis of presence or absence of pubescence is unreliable because of the obvious correlation of pubescence with age. The majority of specimens of both races show evidence of having been minutely appressed-hirsutulous at one time or another.

The stems of both races are simple to the inflorescence; the peduncles of the lateral heads often are extremely elongated and may bear one or more reduced leaves. This tendency appears to be pronounced in *nevadensis*, but it is also present in the species proper and is useless as a key character.

The arrangement of the upper leaves depends upon the total number of pairs of cauline leaves, the position of the leaves on the stem (whether chiefly basal or evenly distributed), and the length of the stem. If the stem bears many leaf pairs, more upper leaves may appear to be alternate; if the leaves are chiefly basal, the number of alternate leaves are few; if the stem is tall, the number of alternate leaves increases. Both races of the species are so variable in these characters that no distinction between them may be made on the basis of leaf arrangement.

Greene's statements regarding the cypselae (akenes) are correct. Jepson,

in reducing *H. nevadensis* to varietal status, separated the two forms on fruit characters alone, thus implying that the presence or absence of a pappus is the only consistent difference between them. The relative depression or elevation of the terminal areola, however, appears to be an imaginary distinction.

7b. **Helianthella californica** var. **shastensis** var. nov.

Herba paena scaposa, 1.0-2.5 dm. alta, glabrata vel plerumque dense breviappresso-pubescens; folia basalia multa, 8-10 (raro 13) cm. longa, linearilanceolata; folia caulina 2-5, omnia linearia, eorum maximo 4 cm. longo 6 mm. lato, foliis superioribus magnopere redactis et bracteiformis; capitulum solitarium, 1.0-1.3 (raro 2.0) cm. latum, radiis omissis; phyllaria lanceolata in basi latissima paucis exterioribus foliaceis; corollae radii breves et latae, 0.5-1.3 cm. longae, discum parum excedentes; cypsela 6 mm. longa, 3-4 mm. lata cuneato-obovata fusca, aristis duobus 1 mm. longis; alae in lateribus angustae in apice lateriores.

Plant almost scapose, 1.0-2.5 dm. high, glabrate or usually densely short-appressed-pubescent; basal leaves numerous, 8-10 (rarely 13) cm. long, linear-lanceolate; cauline leaves two to five, all linear, the largest 4 cm. long, 6 mm. wide, the upper greatly reduced and bractlike; head solitary, 1.0-1.3 (rarely 2.0) cm. broad exclusive of the ray-flowers; phyllaries lanceolate, broadest at the base, a few of the outer ones foliaceous; ray-flowers short and broad, 0.5-1.3 cm. long, little exceeding the disk; cypsela 6 mm. long, 3-4 mm. wide, cuneate-obovate, dull brown, with two awns 1 mm. long; wings narrow on the sides, broader at the apex.

Type locality.—East side, Mt. Eddy, Siskiyou County, California, with *Pinus Jeffreyi*, *Rhamnus*, and *Ceanothus*, July 22, 1916, *Heller* 12489 (Dudley Herbarium).

Distribution.—General vicinity of Mt. Shasta, and nearby Cascade Range, Scott and Trinity Mountains, northern California. (see Map 6)

California. SHASTA CO.: Castella, June 9, 1914, *Smith* 711 (CA, CL-UC,, G, US); the two following collections may be considered to be intermediates between this variety and var. *nevadensis:* Burney, May 23, 1923, Bethel (CA); Goose Valley, June 29, 30, July 11, 1912, *Eastwood* 753 (CA, G). SISKIYOU CO.: east and northeast slopes of spur of Rainbow Ridge above Sulloway Creek 1.5 mi. w. of Mt. Shasta City, 1300 m. alt., June 13, 1936, *Babcock & Stebbins* 1996 (UC); Klamath River, 460 m. alt., June, 1901, *Chandler* 1535 (D, G, M, NY, US); Mt. Bradley, near Shasta Retreat, 1600 m. alt., July 5, 1911, *Condit* (UC); Sisson, July 17, 1912, *Eastwood* 1170 (CA); Shasta Sprs., May 20, 1923, *Eastwood* 11872 (CA); near Sisson, 1160 m. alt., June, 1903, *Hall & Babcock* 4056 (D, F, M, N, P, RM, UC); Shasta Retreat, June 1, 1905, *Heller* 7941 (F, G, IS, M, NY, PA, UC, US); east side, Mt. Eddy, with *Pinus Jeffreyi, Rhamnus,* and *Ceanothus,* July 22, 1916, *Heller* 12489 (D type, CA, F, G, M, NY, OSC, PA, UW isotypes); mountains about the headwaters of the Sacramento River, 2500 m. alt., Aug. 20, 1881, *Pringle* (F, G); Dunsmuir, May 16, 1913, *Smith* (CA, G, US). TRINITY CO.: between Eagle and Bear Creeks, June 25, 1937, *Eastwood & Howell* 4970 (CA, F, US); Scott Mt. Camp, in dry humus over gravel, largely under *Ceanothus* and *Rhododendron,* in shade of pines, 1780 m. alt., *Balls* 13891 (CO).

8. HELIANTHELLA CASTANEA Greene

Helianthella castanea Greene in Erythea 1: 127. 1893. *Helianthella Cannonae* Eastwood in Zoe 5: 82. 1900. *Helianthella castanea* var. *Cannonae* Jepson, Man. Fl. Pl. Calif. 1081. 1925.

Stems low, 1.5-4.5 dm. tall, from slender to stout, repeatedly branched caudices, erect or curved at the base; lowermost pair of leaves usually opposite, the upper cauline leaves alternate, 3-11, oblong to broadly oblanceolate, 10-15 cm. long, 2-5 cm. wide, tapering to petioles one-half as long as the blades, the lower leaves almost equaling the stem in length; head solitary; involucre 2.5-4.0 cm. wide; phyllaries lanceolate, subequal, tapering from base to apex, 1.5-2.0 cm. long, 2-4 mm. wide, conspicuously ciliate on the margins, acuminate, a few of the outermost phyllaries oblanceolate, enlarged and leaf-like; ray-late, enlarged and leaf-like; ray-flowers 3 cm. long, 0.5-1.0 cm. wide, 13-20 in number; disk flowers very numerous (over 100), about 7 mm. long, yellow; receptacular paleae rigid-chartaceous; cypsela glabrous, chestnut-brown, not glossy, plump but thin-edged, 8 mm. long, 6 mm. wide, with short, stout awns; intermediate squamellae obsolete.

Map 7.—Distribution of *Helianthella castanea*

Type locality.—Summit of Mt. Diablo, Contra Costa County, California, collected by E. L. Greene, July, 1892 (Herb. Greeneanum, Notre Dame Univ.).

Distribution. — Grassy hillsides, San Francisco Bay area, California. Blooms in April and May. (Map 7)

California. ALAMEDA CO.: s. side Woolsey Canyon, Berkeley Hills, May 7, 1901, *Chandler* 1024 (UC); near Grizzly, Berkeley, May 10, 1907, *Eastwood* (CA, US): Little Grizzly, May 28, 1933, *Howell* 11379 (CA); Leona Hts., near Oakland, April 22, 1925, *McCalla* (CA). CONTRA COSTA CO.: Mitchel Canyon, Mt. Diablo, May 30, 1915, *Eastwood* 4475 (CA); n. slope of summit, Mt. Diablo, 1200 m. alt., May 31, 1916, *Hall* 10137 (CO, D, P, UC, US); hills e. of St. Mary's College, May 14, 1933, *Howell* 11282 (CA); Pine Canyon, Mt. Diablo, April 21, 1940, *Howell* 15398 (CA); Nortonville, May 12, 1931, *Howell* 6475 (CA, F, G, M, P). SAN FRANCISCO CO.: San Francisco Hills, April 13, 1900, *Brandegee* (UC); Bay View Hills, May, 1899, *Cannon* (CA, type of *H. Cannonae* Eastw.); same locality, May 14, 1920, *Eastwood* (CA). SAN MATEO CO.: Brisbane Hills, April 12, 1941, *Ward* (CA).

The writer has been unable to discover evidence which would justify any taxonomic status whatsoever for *H. Cannonae* Eastwood (*H. castanea* var. *Cannonae* Jeps.).

EXCLUDED NAMES

HELIANTHELLA ALDERSONII Greene in Durand & Jackson, Index Kewensis, Suppl. I: 199. 1906, in error. = *Helianthemum Aldersonii* Greene.

HELIANTHELLA ARGOPHYLLA (D. C. Eaton) A. Gray in Proc. Amer. Acad. 19: 9. 1883. = *Enceliopsis argophylla* (D. C. Eaton) A. Nels.

HELIANTHELLA ARGOPHYLLA Coville in Contrib. U. S. Nat. Herb. 4: 132. 1893. = *Enceliopsis argophylla* var. *grandiflora* (Jones) Jeps. [*E. Covillei* (A. Nels.) Blake.]

HELIANTHELLA COVILLEI A. Nels. in Bot. Gaz. 37: 273. 1904. = *Enceliopsis Covillei* (A. Nels.) Blake.

HELIANTHELLA GRANDIFLORA T. & G., Fl. N. Am. 2: 333. 1842. = *Phoebanthus grandiflorus* (T. & G.) Blake.

HELIANTHELLA IOSTEPHANOIDES Greenman in Proc. Amer. Acad. 40: 41. 1904. = *Pionocarpus madrensis* (Wats.) Blake.

HELIANTHELLA LATIFOLIA Scheele in Linnaea 22: 160. 1849. = *Viguiera dentata* (Cav.) Spreng.

HELIANTHELLA MADRENSIS Watson in Proc. Amer. Acad. 23: 278. 1888 = *Pionocarpus madrensis* (Wats.) Blake.

HELIANTHELLA NUDICAULIS (A. Gray) A. Gray in Proc. Amer. Acad. 19: 9. 1883. = *Enceliopsis nudicaulis* (A. Gray) A. Nels.

HELIANTHELLA PRINGLEI A. Gray in Proc. Amer. Acad. 21: 389. 1886. = *Flourensia Pringlei* (A. Gray) Blake.

HELIANTHELLA TENUIFOLIA T. & G., Fl. N. Am. 2: 333. 1842. = *Phoebanthus tenuifolius* (T. & G.) Blake.

REFERENCES

BABCOCK, E. B. 1949—Supplementary notes on Crepis. II. Phylogeny, distribution, and Matthew's Principle. Evolution 3: 374-376.

BESSEY, C. E. 1915—The phylogenetic taxonomy of flowering plants. Ann. Mo. Bot. Gard. 2: 109-164.

BLAKE, S. F. 1913—A revision of Encelia and some related genera. Proc. Amer. Acad. 49: 346-396.

———1916—Compositae new and transferred, chiefly Mexican. Contrib. Gray Herb. 45: 515-526.

———1918—A revision of the genus Viguiera. Contrib. Gray Herb., n.s., 54. 205 pp.

GARCIA CUBAS, A. 1898—Diccionaria geográphico, histórico, y biográphico de los Estados Unidos Mexicanos, vol. 4. Tulancingo, J. Monter.

GRAY, ASA 1883—Characters of new Compositae, with revisions of certain genera, and critical notes. Proc. Amer. Acad. 19: 1-74.

HEISER, CHAS. B., JR. 1947—Hybridization between the sunflower species Helianthus annuus and H. petiolaris. Evolution 1: 249-262.

———1949—Study in the evolution of the sunflower species Helianthus annuus and H. Bolanderi. Univ. Calif. Publ. Bot. 23: 157-208.

MAGUIRE, BASSETT 1942—Three natural hybrids of the Compositae in Wyethia and Balsamorhiza (abstract). Amer. Jour. Bot. 29: 695.

NELSON, AVEN 1909—Contributions from the Rocky Mountain Herbarium. VIII. Bot. Gaz. 47: 425-437.

OWNBEY, MARION AND W. A. WEBER 1943—Natural hybridization in the genus Balsamorhiza. Amer. Jour. Bot. 30: 179-187.

ROGERS, H. THOMAS 1942—A botanical survey of the upper Columbia River region, Washington. Res. Stud. State Coll. Wash. 10: 99-140.

STOCKWELL, PALMER 1940—A revision of the genus Chaenactis. Contrib. Dudley Herb. 3: 89-168.

TORREY, JOHN AND ASA GRAY 1884—A flora of North America. Vol. II. New York, London, Wiley & Putnam.

U. S. DEPT. OF AGRICULTURE. FOREST SERVICE 1937—Range Plant Handbook. Gov't. Printing Office.

WEBER, W. A. 1946—A taxonomic and cytological study of the genus Wyethia, family Compositae, with notes on the related genus Balsamorhiza. Amer. Midl. Nat. 35: 400-452.

YOUNG, F. G. [Editor.] 1899—The correspondence and journals of Captain Nathaniel J. Wyeth, 1831-1836. [In] Sources of the history of Oregon 1 (parts 3-6), 262 pp. University Press, Eugene, Oregon.

INDEX TO EXSICCATAE

The collector's numbers are indicated in bold face, unnumbered collections by a dash. The numbers in parentheses are those of the species and varieties in this treatment.

Applegate, Elmer I. **264** (7); **2439** (7a).
Babcock, E. B. & G. L. Stebbins, Jr. **1996** (7b).
Bacigalupi, Rimo.—(7); **1719, 2293** (7a).
Bailey, Vernon. **565** (5).
Baker, C. F. **415, 475** (5).
———, F. S. Earle & S. M. Tracy. **645** in part (5).
Baker, Kenneth F.—(4a).
Baker, M. S.—(7a).
Balls, E. K. **13891** (7b).
Beckwith, Florence. **296** (6).
Berghuis, D. P. **8** (4a).
Bethel, Ellsworth.—(6);—(7b).
Bigelow, Dr. J. M.—(7).
Blankinship, J. W. **271** (4);—(7).
Blasdale, W. C.—(7a).
Blumer, J. C. **1442** (5).
Bolt, B. **5845** (7a).
Brandegee, K.—(8).
Brandegee, T. S. **712** (5);—(7a).
Breninger, G. F. **1484** (6).
Brown, H. E. **246** (7a).
Burr, H. J. **114** (4a).
Burtt-Davy, J. **1508** (7a).
Cannon, Evalina.—(8).
Castetter, E. F. **766** (5).
Chandler, Harley P. **1535** (7b); **1024** (8).
Chase, V. H. **7675** (3a).
Christ, J. H. **5158** (4).
Clements, Fred. **56** (5); **151** (6).
Clements, F. E. & E. S. Clements. **187** (6).
Cleveland, D.—(7).
Clokey, I. W. **2846, 3135** (5).
Condit, I. J.—(7b).
Constance, L. **2301** (7a).
Constance, L., A. Dimond, R. C. Rollins & C. Worley. **1120** (4a).
Copeland, E. B. **695** (7a).
Coville, F. V. & J. B. Leiberg. **52** (5).
Cowen, J. H. **714** (5).
Crandall, C. S. **471** (4).
Cronquist, Arthur. **318-36, 665-37, 1635, 1764, 2358** (4); **827-37, 1726** (5).
Curtis, C. C.—(4);—(5).
Cusick, W. C. **1680** (4a).
Cutler, Hugh C. **3054** (1); **2452** (4).
Dandelin, J. E.—(6).
Darrow, R. A., W. S. Phillips & L. M. Pultz. **1074** (5).
Davis, Ray J. **2748, 2852, 3970** (4); **2247** (4a).
Diehl, I. E.—(6).
Dillon, Mildred & Louis A. Dillon. **631** (4a).
Dobrinz, Edward. **49** (4).
Eastwood, Alice.—(5);—(6);—, **3341** (7); **535, 14555** (7a); **753, 1170, 11872** (7b);—, **4475** (8).
——— & J. T. Howell. **6365a, 6750** (1); **4533, 5736** (7); **4970** (7b).
Eggleston, W. W. **8109** (4); **12293, 13528** (4a); **5781, 10348** (5); **5994, 17051, 19004, 19177** (6); **9186, 22191** (7a).
Eikenberry, W. L. **2** (4).
Elmer, A. D. E. **4488** (7).
Evans, H. M.—(7a).
Favre, C. **258** (5).
Ferris, Roxana & Rena Duthie. **938** (4a).
Fiker, Charles B. **219** (4a).
Fisher, George L. **36156, 38175** (5).
Flodman, J. H. **871** (4); **872** (5).
Garrett, O. A. **7861** (1).
Gierisch, Ralph K. **1043, 1055** (6).
Goodding, L. N. **265** (5).
Goodman, George J. **1853** (4).
Gould, Frank W. **1887** (4); **1031** (7).
Graham, Edw. H. **8664, 9732** (4); **8341, 9540** (5).
Griffiths, David. **5266** (6).
——— & E. L. Morris. **450** (4).
Grinnell, Fordyce. **271** (7a).
Gustafson, Theodora.—(4a).

Hall, H. M. **10137** (8).
——— & E. B. Babcock. **4411** (7a); **4056** (7b).
Hanks, Chas. W. **24** (7a).
Hansen, G. **167** (7a).
Harrison, B. F. & A. O. Garrett. **8882** (1).
Hayward, Herman E. **2320, 2743** (5).
Heller, A. A. **9050, 11108** (4);—(4a); **8522** (7); **7006, 11897** (7a); **7941, 12489** (7b).
——— & H. E. Brown. **5192** (7).
——— & Gertrude Heller. **3292** (4a).
Henderson, L. F. **8562** (4a).
Hermann, F. J. **5644** (5).
Hester, J. Pinckney. **1026** (1).
Hillman, F. H.—(7a).
Hitchcock, Albert E. **1276** (4).
Hitchcock, C. Leo. **16966** (4); **8101** (4a); **16731** (5); **6392** (7a).
——— & J. S. Martin. **5670** (4).
——— & C. V. Muhlick. **9757, 10229, 10384, 12430, 12565, 13009, 13332, 15251** (4); **8444, 13883** (4a); **12459, 13461, 13602** (5).
———, Roland V. Rethke & R. van Raadshooven. **3886, 4597** (4); **4137, 4161** (6).
Holway, E. W. D.—(5).
Hooker, J. D. & A. Gray—(6).
Horner, R. M. **B-280** (4a).
Howell, J. T. **6704, 13057** (7); **378, 12561** (7a); **6475, 11282, 11379, 15398** (8).
Howell, Thomas.—(4a).
Huber, Wharton.—(5).
Jepson, Willis Linn.—(7).
Johnson, K. Richard. **716** (4).
Jones, George Neville. **4039** (4a).
Jones, Marcus E.—, **1177, 1178** (4); —, **6404, 25067** (4a); **5686** (5);—(7a).
Jones, Wyatt W. **507** (4).
Kearney, T. H. & R. H. Peebles. **12275** (5).
Keck, David D. **1651** (7a).
Kelsey, F. D.—(4).
Leiberg, J. B. **1017** (4a); **4191** (7a).
Le Sueur, Harde. **156, 157, 244** (2); **1004** (5).
Letterman, George W.—(6).
Lister, Paul B. **94** (6).
Livingston, B. E. & J. J. Thornber. —(5).
Lommasson, Thomas. **62** (4a).
Loughridge, Gasper A. **262** (5).
Lundell, C. L. **5387** (3).
Macbride, J. F. **457** (4).
MacDougal, D. T. **312** (5).
Mackenzie, K. K. **89** (5).
Macoun, John.—, **46, 974** (4a).
Maguire, Bassett. **3154** (4); **12473, 12479** (5); **17221** (7a).
———, Ruth Hobson & Ruth Maguire. **14241** (4).
——— & Arthur Holmgren. **22671** (5).
———, George Piranian & B. L. Richards, Jr. **12898** (4).
———, A. G. Richards, Ruth Maguire & Ruth Hammond. **18007** (5).
Maris, H. B. **154, 222** (4).
McCalla, W. C.—(8).
McDonald, Chas. H. **20** (5).
McIntosh, A. C. **698** (5).
McMurphy, I. J.—(7).
McNair, A. D. **112** (6).
Metcalfe, O. B. **513, 1435** (5).
Meyer, F. G. **402** (4a).
Moxley, Geo. L. **543** (7a).
Mueller, C. H. **2277** (5).
——— & M. T. Mueller. **353** (3a).
Muenscher, W. C. **9026** (4a).
——— & M. W. Muenscher. **15961** (4a).
Mulford, A. Isabel.—(5).
Munz, P. A. **16983** (5); **13336** (7).
Murley, Margaret. **1676** (4a).
Nelson, Aven. **7713** (4); **803, 2899, 7301, 8903** (5).
——— & J. F. Macbride. **1041, 1207, 1797, 2004** (4).
——— & E. Nelson. **6409** (5).
Nelson, E. W. **4808** (5).
Newberry, Dr.—(1).
Nielson, R. D. **30** (4).
Noble, M. & H. Andrews.—(1).
Oleson, O. M. **122** (4).
Olsen, Ray.—(4).
Osterhout, G. E. **2689, 3854, 7921** (5).
Over, W. H. **16233** (5).
Ownbey, Marion. **1434, 1476** (1).
——— & Fred G. Meyer. **2320** (4a).
Packard, Jacqueline. **440** (4a).
Palmer, Dr. E. **601** (3a); **106B** (7a).
Pammel, L. H. & R. E. Blackwood. **3879** (4).
———, C. P. Johnson, R. E. Buchanan & G. W. Lummis. **1977** (4).

Parker, C. S. **699** (4a).
Parker, Kitty F. **5944** (5).
Parker, K. F., F. McClintock & G. T. Robbins. **6245** (1).
Parry, C. C.—(6).
——— & Edw. Palmer. **463** (3).
Payson, Edwin B. **591** (1); **525** (5).
Payson, E. B. & George M. Armstrong. **3316** (4).
——— & Lois B. Payson. **4218** (1); —(4); **3939, 5107** (5).
Pearson, E. & D. Pearson. **144** (4).
Pechanec, Joseph. **21** (4).
Peck, Morton E. **4935** (4); **10136, 18240, 22389** (4a).
Penfound, Wm. **133** (6).
Peterson, Jesse L. **270** (4a).
Phillips, J. L. **70** (4).
Piper, C. V. **1598** (4a).
Porter, T. C.—(6).
Post, U. J. **288** (5).
Pringle, C. G.—(7b).
Purpus, C. A. **6214** (4).
Ramaley, Francis. **1330, 15267, 15555, 15658, 15685, 16647** (6).
Ramaley, F. & Joseph A. Ewan. **16692** (5).
——— & W. Gambill, Jr. **16917** (6).
Read, A. D. **27** (5).
Reid, E. H. & Robert Collins.—(4a).
Reid, E. H. & E. Henderson. **433** (4a).
Renner, Frederic G. **1186** (4a).
Robbins, G. T. **1042** (7a).
Rollins, Reed C. **1948** (1).
——— & T. S. Chambers. **2562** (4).
Rose, Lewis S. **32430** (5); **41246** (7); **34366** (7a).
Rydberg, P. A. **6072** (4); **807** (5).
——— & Ernst A. Bessey. **5178** (4).
——— & E. C. Carlton. **7124** (4).
——— & A. O. Garrett. **9470** (1); **9004, 9716** (5).
St. John, Harold. **3375** (4a).
Saling, W. M. **22** (5).
Sandberg, J. H. & John B. Leiberg. **486** (4a).
———, D. T. MacDougal & A. A. Heller. **321** (4a).
Schaffner, J. H. **304** (3).
Schmoll, Hazel M. **342, 1527** (5).
Schneider, Richard A. **1002** (3a).
Shafer, Paul. **19** (4).
Sharples, S. P. **266** (4a).
Sharsmith, H. K. **1035** (7).
Shaw, W. T.—(4a).
Shear, C. L. **4135, 4140, 5098** (5).
Sheldon, C. S. **151** (5); **5834** (6).
Shipley, M.—(4).
Shreve, Forrest. **8033** (5).
Smith, Frank H. **66** (5).
Smith, George R.—(5).
Smith, L. E.—, **711** (7b).
Smith, L. S.—(7a).
Standley, Paul C. **7350** (1); **4266, 6775, 7555** (5); **4684, 13379, 14362** (6).
Stanford, L. R., K. L. Retherford & R. D. Northcraft. **398, 654, 738** (3a).
Stewart, John. **43** (5).
Stigall, B. M.—(5).
Sturgis, W. C.—(4).
Suksdorf, Wilhelm N. **484-M, 566-M, 639-M** (4); **524, 6350, 10077, 13076, 13098** (4a).
Swenson, J. C. **96** (4).
Swift, Lloyd W. **55, 92** (7a).
Taylor, W. P. & C. H. Richardson. **1** (5).
Thompson, C. P. **14** (4).
Thompson, J. W. **4733, 6486, 7039, 11591, 11724, 12020** (4a).
———, & E. M. Thompson. **133** (4a).
Thornber, J. J. & Forrest Shreve. **7758** (5).
Towne, C. R. **61** (4).
Train, Percy.—, **241, 477, 514** (4).
Tweedy, Frank. **4054** (4); **326, 2056, 4055, 5860** (5).
Walker, Ernest P. **367** (1).
Ward, G.—(8).
Ward, L. F. **524** (1).
Ware, E. R. **261** (5).
Watson, Sereno. **605** (4).
Weber, W. A. **2226** (4a).
Wherry, E. T. **3722** (5).
Whited, Kirk. **663** (4a).
Williams, Louis O. **816, 1209** (4).
Williams, L. O. & Rua Williams. **3254** (5).
Willits, Vie. **224** (5).
Wolf, Carl B. **3029** (5); **5102** (7a).
Wolf, John & J. T. Rothrock. **546** (5).
Woods, C. N. **359** (4).
Woolley, Sam. **16** (4).
Wooton, E. O.—(5):—(6).
Yuncker, T. G. **5418** (4).

Carex acutiformis in Indiana

F. J. Hermann

Plant Industry Station, Beltsville, Maryland

The Eurasian and African sedge, *Carex acutiformis* Ehrh. is said by Mackenzie to be "very locally naturalized from Europe in eastern Massachusetts," where he ascribes it to "boggy meadows" (N. Amer. Flora 18: 436. 1935). Most nearly related to *C. lacustris* Willd. and *C. hyalinolepis* Steud. among our native species, it may be readily distinguished from these by its flattened perigynia with very short (0.5 mm. or less long), shallowly bidentate or emarginate beak. In the eighth edition of *Gray's Manual of Botany* the American occurrence of this strikingly handsome sedge is given in the text as "boggy meadows and borders of saline marshes, local, e. Mass.," while in the key the species is said to be a "local adventive near Boston," but the only definite locality record I find is that published by the Committee on Local Flora, New England Botanical Club in Reports on the Flora of the Boston District, — XII (Rhodora 13: 233. 1911): "salt marsh by Old Colony R. R. at Savin Hill, Dorchester, from 1865 (*Wm. Boott*) to 1888 (*E. & C. E. Faxon*); station now extinct (*J. R. Churchill*)." Consequently the discovery, almost a century later, of a thriving colony of the species in northern Indiana by Father P. E. Hebert is an unexpected and noteworthy record. Father Hebert collected it twice on the margin of St. Joseph Lake, Notre Dame, St. Joseph County, first on May 26 then on June 12, 1951, where he reports two stations for it. One of these is on the south shore, comprising a hundred or so plants extending for some twenty-five or thirty yards along the marly lake-margin. The other locality, about seven hundred yards away, is on the northeast shore, where the soil is sandy, limy and gravelly, and here the colony is about fifty yards in extent and includes two hundred or more plants. Neither of the two collections seen have fully mature perigynia so that the plant probably does not reach its prime here until nearly the first of July. The specimens upon which the new record is based were kindly loaned to the writer for examination and are deposited in Father Hebert's private herbarium at the University of Notre Dame.

Notes on Wisconsin Parasitic Fungi. XV.

H. C. Greene

Department of Botany, University of Wisconsin, Madison

This series of notes is, with some exceptions, based on collections made during the seasons of 1949 and 1950.

The phytoplankton of Wisconsin lakes, particularly the *Bacillariaceae, Desmidiaceae* and *Volvocaceae,* as well as some of the filamentous algae, including *Spirogyra, Zygnema* and *Mougeotia,* are rather frequently parasitized by chytridiaceous fungi, but determination of these forms, owing to their small size and transitory nature, is all too often highly uncertain. A. F. Bartsch, in a doctoral thesis (Univ. Wis. 1939) entitled "A Taxonomic Study of the Aquatic Chytridiales," lists for the state about twenty possible parasites, some very doubtfully so, mostly on filamentous algae, and a few on water molds and pollen grains.

Powdery mildews which did not form perithecia and are hence indeterminable were noted on 1) *Brassica arvensis.* Dane Co., Madison, September 10, 1950, and 2) *Verbena hybrida* (cult.). Dane Co., Madison, September 25, 1949.

MICROSPHAERA ALNI (Wallr.) Wint. occasionally infects leaves of *Ceanothus americanus* without evidence of any particular damage to the host plants. However, in August 1949 the developing fruits of many large specimens of *Ceanothus* in the University of Wisconsin Arboretum at Madison were devastatingly blighted by a powdery mildew which did not form perithecia, but which I assume was *M. alni.* So heavy was the infection that, at a distance, the plants appeared to be still in full bloom, with characteristic white flower clusters.

MYCOSPHAERELLA, so far undetermined, occurred in profuse development on overwintered leaves of *Botrychium virginianum* collected in May 1950 in the New Glarus Woods in Green Co. In my Notes XIV the immature phase of the fungus was described as being actively parasitic on the still green leaves in August 1949. The fungus appears to have had a preservative influence, since in the spring only heavily infected leaves were found, whereas in a section of the woods in which no infection was noted the previous summer, no overwintered leaves could be found. When the overwintered material was first examined it was found that, while asci had been delimited, mature ascospores were not yet formed. Accordingly, the leaves were placed in a moist chamber for 72 hours, when it was noted that well-developed ascospores had been produced. The perithecia are subglobose to globose, black, mostly about 60-80μ diam.; the clavate asci are 7-8 x 30-40μ; the hyaline, uniseptate, slightly curved ascospores are 10-12 x 3-3.5μ. There was no evidence of any well-defined imperfect stage preceding the *Mycosphaerella,* although in the August 1949 collection certain of the perithecial bodies contained bacillary microconidia about 4 x 1μ.

MELAMPSORA OCCIDENTALIS Jacks. is reported in Arthur's Rust Manual as occurring on *Populus balsamifera* in Wisconsin. However, the range is given as "British Columbia and southern California eastward to Wyoming." The citation of Wisconsin as a host locality is based on Fungi Columbiani 3915 which is labeled as *Melampsora medusae* on *Populus balsamifera*, collected at Madison. Examination of the specimen shows that it has urediospores the larger of which are well outside the size limits specified for *M. medusae* and equal or exceed those of *M. occidentalis*. Since the latter species does occur on *Populus balsamifera* in the far west, and since this tree is not native to the near vicinity of Madison, it seemed possible that the infected tree might have come from western nursery stock set out for ornamental purposes. The question was posed to G. B. Cummins, now Curator of the Arthur Herbarium, and he is currently of the opinion that the specimen fits neither *M. medusae* nor *M. occidentalis* very well. He thinks it is probably closer to *M. medusae* since 1) the general run of urediospores are smaller than in typical *M. occidentalis* and less robust, 2) the thickened side walls have smooth areas, 3) the teliospores come nearer the length of *M. medusae*, although some reach 55μ, and 4) the apical wall of the teliospore is not thickened. Aside from the Fungi Columbiani specimen, *M. medusae* has not been reported as being on *Populus balsamifera* in Wisconsin.

PUCCINIA STIPAE Arth. I was produced on *Aster ericoides* (*multiflorus*) in a greenhouse infection experiment by the late J. J. Davis (Trans. Wis. Acad. Sci. 20: 422. 1922) in minimal amount, using teliospores from *Stipa spartea*, but he made no field collections. In June 1950 near Brodhead, Green Co., good material was collected on plants of *Aster ericoides* growing in the midst of *Stipa spartea*.

AECIDIUM CAMPANULASTRI G. W. Wils., which occurs on *Campanula americana* in Wisconsin and neighboring states, is one of the few such American rusts whose complete life history is still unknown. Attempts by me to infect plants of *Campanula americana*, using over-wintered teliospores of *Puccinia extensicola* (*P. extensicola phrymae* (Halst.) Arth.) and *P. caricis* (*P. caricis grossulariata* Arth.), have so far failed

PHYLLOSTICTAE of uncertain affinities, and concerning whose parasitism there is often a question, continue to be found on various hosts in Wisconsin. Descriptive notes on some of these are here given: 1) On *Cystopteris bulbifera*. Sauk Co., Baxter's Hollow, Town of Sumpter, August 30, 1949. The fungus is on small, whitish, thin, translucent spots on the living green leaves. Pycnidia are sooty, subglobose, approx. 50-65μ diam., the hyaline conidia 3.5-6 x 1.5-2μ. This does not appear secondary and was probably parasitic. 2) On *Andropogon furcatus*. Dane Co. near Belleville, September 1, 1950. The affected leaves are brown and dead, and there are no well-marked spots, although some areas are lighter than others. Pycnidia are epiphyllous, lenticular, pale brown, approx. 125μ in long diam. x 60μ in short diam., the hyaline conidia cylindric to subfusoid, large, 12-18 x 4.5-5μ. So far as observed, there is no hint of septation in any of the conidia. 3) On *Habenaria leucophaea*. Dane Co., Madison, August 11, 1950. The rounded or angled

spots are 4-5 mm. diam., with pale brown centers and rather wide dark margins. Pycnidia are epiphyllous, dark brown, flattened, about 125μ diam., the hyaline conidia 4-6 x 2.5-3μ. 4) On *Polygonum convolvulus*. Dane Co., Madison, July 11, 1946. On irregular, immarginate, reddish-brown dead areas, involving not more than a quarter of the leaf. Pycnidia are amphigenous, mostly epiphyllous, scattered to gregarious, or sometimes closely clustered, black, subglobose, widely ostiolate, approx. 125-175μ diam. Conidia are hyaline, subfusoid, 6-10 x 3-3.5μ, with many showing a med an pseudoseptum after clearing in mounting fluid. Conidiophores are well-differentiated, slender, flask-shaped, 6-8μ long. The conidia are of the type usually found in *Phomopsis*, but scolecospores were not seen. 5) On Japanese barberry, *Berberis thunbergii*. Dane Co., Madison, July 29, 1950. The more or less elongate spots are grayish-brown with a red border and a shredding of the lesion occurs. Pycnidia are somewhat superficial, amphigenous, dark brown, of variable diam., from 80-150μ. Conidia hyaline, subcylindric, 5-7 x 3μ. 6) On *Amorpha fruticosa*. Dane Co., Madison, September 5, 1949. The lesions are of two types: *a*. rounded or ellipsoid spots, 2-8 mm. diam., with ashen centers and rather wide blackish-brown borders, and *b*. dead areas, involving the leaflet tips, back for as much as 7 or 8 mm., which are a uniform brown with less distinctly defined margins. On both types of lesion the pycnidia are epiphyllous, gregarious, subcuticular, sooty-brown, somewhat flattened, subrostrate, 50-115μ diam. Conidia hyaline, subcylindric, 4-7 x 2.5-3μ. The rounded lesions appear to have been produced by the parasitic activity of the fungus, but the dead tips give the impression of a secondary development and the relationship of fungus and host is thus unclear. 7) On *Desmodium bracteosum* var. *longifolium*. Green Co., New Glarus Woods, June 6, 1949. Spots small, brown, angled. Pycnidia few on a spot, epiphyllous, succineous, subglobose, with thin, pale brown, pseudoparenchymatous walls, mostly about 150μ diam. This is not *Phyllosticta desmodii* Ell. & Ev. Perhaps the precursor of a perfect stage. The microconidia, 3-4 x 1.5μ, suggest this. 8) *Mentha arvensis* var. *canadensis*. Dane Co., Madison, August 29, 1949. Pycnidia are large, up to 250μ diam., on rather large brownish spots which tend to become confluent in severely infected leaves. Conidia hyaline, 6-10 x 2.5-3μ. This is not *Phyllosticta decidua* Ell. & Kell., nor does it seem to be *P. monardae* Ell. & Barth., described as with conidia 5-6 x 1.5μ, and previously reported by me as occurring on *Mentha* in Wisconsin. I suspect that a series of transitional forms between the small-spored *P. monardae* and the fungus mentioned in this note will eventually be found. 9) On *Aster linarifolius*. Green Co., Sect. 1, Town of Sylvester. August 4, 1950. The whitish spots are rounded, isodiametric or somewhat elongate, usually extending from the margin to the midrib of the narrow leaf. Pycnidia are epiphyllous, gregarious or scattered, conspicuous, deep brown, subglobose, about 150-200μ diam. Conidia hyaline, ellipsoid, 5-7 x 2.5-3.5μ. The spots are very numerous, but many bear no pycnidia. 10) On *Gaillardia pulchella* var. *picta*. Dane Co., Madison, September 17, 1950. The conspicuous spots are rounded, 4-10 mm. diam., more or less sunken, gray, with narrow, darker borders.

Pycnidia are epiphyllous, gregarious, blackish-brown, globose, approx. 125-150μ diam. Conidia hyaline, ellipsoid, 4-5 x 2-2.5μ.

PHYLLOSTICTA PRUNICOLA Sacc. has been reported on *Prunus nigra* and *P. serotina* in Wisconsin. It has conidia about 5 x 3μ as shown by specimens. In addition, *Phyllosticta serotina* Cooke has been reported on *Prunus serotina*, but examination of a specimen so labeled and collected by Davis at Racine in 1888 reveals that its conidia are the size of those of *P. prunicola*, instead of being 12 x 3μ as in Cooke's species. Trelease mentioned an undetermined *Phyllosticta* with ellipsoidal hyaline conidia, 2-4 x 7-8μ, which would seem intermediate. Evidently, *Phyllosticta serotina* Cooke should no longer be included in the Wisconsin lists.

PHYLLOSTICTA LIATRIDIS J. J. Davis was described as having pycnidia 65μ diam. and conidia 10 x 4μ. Collections on various species of *Liatris* which seem referable to this species in most cases have had pycnidia larger than 65μ, but with conidia about as described. In a specimen from Madison, July 1, 1948, on *Liatris cylindracea*, the pycnidia are exceptionally large, mostly about 175μ and a fair percentage of the conidia (most of which are about 10 x 4μ or slightly longer) have a median septum.

CONIOTHYRIUM sp. is on sharply defined, rounded, red-bordered, tan spots on living leaves of *Cyperus erythrorhizos*, collected August 20, 1948 at Ferry Bluff, Sauk Co. The fungus appears parasitic, although the specimen is small and inadequate. The pycnidia are about 125μ diam., the ellipsoid, olivaceous conidia 7-10 x 3-4μ. Another undetermined species of *Coniothyrium* occurs on narrowly elongate brown areas on leaves of *Cypripedium pubescens* collected June 16, 1949 at a station in the Town of Exeter, Green Co. The pycnidia are about 75μ diam., the smoky conidia mostly 4-6 x 3-4μ. Parasitism doubtful.

ASCOCHYTA ACTAEAE (Bres.) Davis (Trans. Wis. Acad. Sci. 19 (2): 698. 1919) will, I think, be found, when fully developed, to be a species of *Stagonospora*. A collection on *Actaea rubra*, from Parfrey's Glen, Sauk Co., is just short of a well-defined x-septate condition.

ASCOCHYTA sp., on *Trifolium procumbens* at Madison, July 2, 1949, has not been satisfactorily identified with any of the *Ascochyta-Stagonospora* series occurring in Wisconsin on other species of *Trifolium*. From *Stagonospora recedens* (C. Massal.) Jones & Weimer (*Ascochyta trifolii*) as it occurs on *T. pratense*, the form on *T. procumbens* differs in having conidia only 3-3.5μ wide, instead of 5-6μ. From well-developed *Stagonospora meliloti* (Lasch) Petr. it differs in having no conidia with more than one septum, although the conidia are markedly longer than wide, many being as much as 20μ. On the basis of lesion type and host relationship it seems possible that this represents a poor development of *Stagonospora meliloti*.

ASCOCHYTA sp. is exceptionally well-marked in a small, inadequate specimen on tiny white spots on leaves of *Ambrosia trifida* from Madison, September 24, 1949. The dark brown pycnidia are about 150μ diam., with the large ostiole, 20μ diam., marked by a ring of dark cells. The conidia are 10-13 x 3.5-5μ. Many are strongly constricted at the septum.

STAGONOSPORA on a cultivated species of *Thalictrum* (not *T. dasycarpum*), collected at Madison, July 27, 1950, has very distinctly septate spores, mostly 1-septate, but many 2-septate, about 14-23 x 5μ. This is another in a large series of the *Ascochyta-Stagonospora* group collected on *Thalictrum* and other Ranunculaceae in Wisconsin, concerning which Davis (Trans. Wis. Acad. Sci. 19 (2): 698. 1919) stated "Such series on the same or on related hosts seem to be not uncommon, but there appears to be no way in the present state of taxonomy to indicate the relationships by grouping them, especially as increased spore length often brings increased septation and thereby passes generic limits as now understood." Davis made a collection on *Thalictrum dasycarpum* at Saxon, Iron Co., in which the spores were 10-17 x 3-4μ and which he assigned to *Ascochyta clematidina* var. *thalictri* Davis, although the spores were larger than described by him.

STAGONOSPORA sp., mostly immature, occurs on leaves of *Amphicarpa bracteata* (*monoica*) collected at Madison, September 8, 1948. The spores are 0-2-septate, 4-13 x 3-4μ. Most are continuous, a good many are 1-septate, and only a few are 2-septate. The flesh-colored pycnidia, mostly rather large, up to 200μ diam., are borne on rounded spots with a water-soaked appearance, or on larger brownish dead areas. Pycnidia from the rounded spots show many more conidia with septation.

SEPTORIA CARICINELLA Sacc. & Roum. has been reported on a number of species of *Carex* in Wisconsin. I have not been able to examine any authentic European material of this species. The Wisconsin specimens almost uniformly have pycnidia which are so widely open as to suggest *Phleospora*. No mention of such a feature is made in the description of *S. caricinella*. At present there are not sufficient grounds for renaming the Wisconsin material, but I think it probable that it differs from that on which the species was based. Sydow's Mycotheca germanica No. 2750, distributed as *Septoria caricinella*, turns out to be, as is so frequently the case with later examples of that series, something quite different, perhaps *S. caricicola* Sacc.

GLOEOSPORIUM sp. occurs on sharply defined, rounded, cinereous spots on the leaves of *Coptis trifolia*, collected by E. H. Varney near Sturgeon Bay, Door Co., August 1950. On the basis of spore measurements this can scarcely be *Gloeosporium aquilegiae* Thum., which seems to be the only species reported on a closely related host. The small, punctate, closely clustered acervuli are overlaid with pinkish masses of the hyaline, ellipsoid conidia.

BOTRYTIS of one or more species, acting possibly parasitically, was found on a number of hosts in the season of 1949, the early part of which was notable for high humidity combined with high temperatures. Beside a number of liliaceous hosts, mentioned in the series of notes preceding this, *Impatiens biflora* and *Polygonum scandens*, both collected at Madison, bore heavy infections. On *Impatiens*, particularly, the fungus appears parasitic. It is on very well-marked, rounded, zonate areas, about 1 cm. diam., and there seems to be no other organism involved. I have been unable to determine these specifically.

CERCOSPORELLA BRASSICAE (Fautr. & Roum.) Hoehn., or something very

similar, occurred in scanty amount on leaves of *Cakile edentula*, collected near Oostburg, Sheboygan Co., October 9, 1949. The small spots were sharply delimited, but any final conclusion as to parasitism must await collection of more material.

CERCOSPORA sp. was found in small amount on the calyx of *Psoralea esculenta* from near Arena, Iowa Co., August 1, 1950. The small oval spots are ashen with a narrow, but prominent, brown border. The closely tufted phores are non-septate, straight or once-geniculate, brownish below, with colorless tips and prominent spore scars, about 40-50 x 4μ. The dilutely fuliginous conidia are narrowly obclavate, mostly 7-10-septate, 55-120 x 3.5-4μ.

CERCOSPORA sp., which bears no resemblance to the *Cercosporella* commonly occurring on *Saxifraga* in Wisconsin, was collected on leaves of *S. pennsylvanica*, in small quantity, at Exeter, Green Co., September 1, 1950. The spots have cinereous centers and prominent dark-reddish borders, and are rounded to ellipsoid, about 3-5 mm. diam. The conidiophores are few, in loose, spreading tufts. They are epiphyllous, variable in length, from 65-375μ, and from 4-6μ wide at the base. They are sooty gray above, grading through a pale brown in the central portion to a fairly deep brown at the base in the longer phores, several-septate, not markedly geniculate, truncate at apex with a prominent spore scar. The conidia are likewise exceptionally long, up to nearly 400μ. They are slender clavate at base, about 4μ, tapering rapidly to filiform above, laxly curved, pale fuliginous, closely multiseptate, abruptly truncate at base with a prominent spore scar. I find no record of a *Cercospora* on *Saxifraga*.

CERCOSPORA PARVIMACULANS J. J. Davis must be considered a synonym of *Cercospora stomatica* Ell. & Davis, according to Chupp, who recently has examined most of the many Wisconsin specimens on various species of *Solidago*. It had been my impression that *C. stomatica*, as it occurs on *Solidago latifolia*, was probably distinct from a similar form which appears on a number of other species of *Solidago* in Wisconsin, including *S. altissima*, *S. gigantea* (*serotina*), *S. juncea*, *S. riddellii*, *S. rigida* and *S. uliginosa*. Chupp states in part "I believe all of them are *C. stomatica* and that they can be included in the following description, even though the various *Solidago* species have different types of lesions. For instance, those on *S. serotina* are small and numerous, while those of *S. latifolia* are few and relatively large. Some are uniform in color, some have a minute pale tan to white center, while others have a large dark brown necrotic area. Certain spots have a distinct margin with the dead tissue immediately adjoining the green. Others have a yellow or purple halo that gradually fades into the healthy tissue. But with all the variation in lesion, the fungus (judging from my own standards) is the same on each *Solidago*. Stromata are lacking or composed of only a few dark brown cells. The fascicles are composed of 2 to 14 divergent, coarse conidiophores which are pale to medium brown or olivaceous brown, uniform in color, rarely attenuate toward the subconic tip, 1-7-septate, not branched, straight to tortuous or abruptly geniculate, 4.5-7 x 20-180μ, usually 20-80μ;

conidia subhyaline to pale olivaceous, distinctly obclavate to obclavate-cylindric, multiseptate, straight to mildly curved, base subtruncate or rounded to long obconically truncate, tip obtuse, 4.5-6 x 40-180μ. I believe all your packets labeled *C. stomatica* and *C. parvimaculans* agree with this description of the fungus" Beside *C. stomatica* there is only one other known species of *Cercospora* on *Solidago* in Wisconsin, namely *C. solidaginis* Chupp & Greene, so far collected on *S. juncea* and *S. missouriensis* var. *fasciculata*.

CERCOSPORA APII Fres. is the species name used by Johnson and Valleau (Phytopath. 39: 763. 1949) in lumping 44 species names as synonyms. This includes such well-known names as *Cercospora nicotianae* Ell. & Ev., *C. althaeina* Sacc., *C. avicularis* Wint., *C. beticola* Sacc., *C. diffusa* Ell. & Ev., *C. omphacodes* Ell. & Holw., *C. physalidis* Ell., *C. plantaginis* Sacc., *C. polygonacea* Ell. & Ev. and *C. violae* Sacc. The authors state that cultures were obtained from 28 species in 16 plant families, and that the isolates from the various hosts could not be distinguished by colony characters or by spore size and shape. They say that typical frogeye of tobacco developed on tobacco inoculated with isolates from 16 species in 11 families, and that similar results were obtained on other species of plants. All the original host plants were growing adjacent to plots of *Cercospora*-infected tobacco. Johnson and Valleau are undoubtedly right in asserting that too much emphasis has been placed on hosts in delimiting species of parasitic fungi. Work such as theirs may ultimately result in far-reaching nomenclatorial revisions, particularly within the Fungi Imperfecti.

CERCOSPORA SEQUOIAE Ell. & Ev. var. JUNIPERI Ell. & Ev. is the name that was applied to a *Cercospora*-like fungus, first noted on the foliage of *Juniperus virginiana* near Kenosha,, Wis. The same fungus also is found on *Juniperus communis* var. *depressa* in this state. As I pointed out in an earlier note (Trans. Wis. Acad. Sci. 38: 283. 1946), Chupp considers that this is not properly placed in *Cercospora*. Accordingly I referred the fungus to *Exosporium deflectens* Karst., despite discrepancies in conidial measurements. Recently received material, collected in Michigan and plainly the same as the Wisconsin oragnism, is labeled *Exosporium glomerulosum* (Sacc.) Hoehn. which, I assume, is a n. comb. for the fungus described by Saccardo as *Clasterosporium glomerulosum*, although I have been unable to determine where the new name was published. Conidial measurements given for these fungi in the Saccardian descriptions are as follows: *Cercospora sequoiae* var. *juniperi* —15-30 x 3μ; *Exosporium deflectens*—3-septate, 14-20 x 5-6μ; *E. glomerulosum*—6-7-septate, 35-45 x 8-10μ. The Wisconsin and Michigan specimens do not approach a width of 8-10μ. Most of the conidia are about 3-5μ wide, but are quite variable in length and septation, especially in the Wisconsin material. The specimens distributed by Petrak as *Exosporium glomerulosum* on European *Juniperus communis* are in poor condition and of no assistance in reaching a decision on the American fungus. It may be that the latter is not really referable to *Exosporium deflectens*, but since I have not been able to examine an authentic collection of that species, it is perhaps best to let the matter rest for the time being.

ADDITIONAL HOSTS

The following hosts have not been previously recorded as bearing the fungi mentioned in Wisconsin.

ALBUGO BLITI (Biv.) O. Ktze. on *Amaranthus graecizans*. Dane Co., Madison, August 9, 1910. Coll. I. E. Melhus. Davis placed this specimen in the herbarium, but did not report it. The host is in good fruiting condition and is correctly determined.

SCLEROSPORA GRAMINICOLA (Sacc.) Schroet. on *Zea mays*. Door Co., Sturgeon Bay, July 8, 1921. Coll. R. B. Streets. Davis seems to have omitted this from his notes and indices, so it is here very belatedly included to complete the record, in the attempt to encompass all reports of fungi parasitic on plants in Wisconsin within these notes from the Herbarium of the University of Wisconsin. Weston (Phytopath. 19: 392. 1929) published a rather detailed article dealing with the occurrence of this mildew on corn in Wisconsin.

SPHAEROTHECA HUMULI (DC) Burr. on *Rosa carolina*. Dane Co., Madison, September 21, 1949. Also on *Humulus japonicus*. Dane Co., Madison, October 9, 1949. (It appears highly probable that an earlier report of this fungus on *Humulus americanus* was incorrect and that the host in that case also was *H. japonicus*.)

SPHAEROTHECA HUMULI var. FULIGINEA (Schl.) Salm. on *Veronica spicata* (cult.). Dane Co., Madison, September 22, 1949.

MICROSPHAERA ALNI (Wallr.) Wint. on *Viburnum opulus* (cult.). Dane Co., Madison, October 8, 1950.

MICROSPHAERA DIFFUSA Cke. & Peck on *Asclepias tuberosa*. Dane Co., Madison, September 22, 1950. There seem to be no previous reports of this species on *Asclepias*.

ERYSIPHE POLYGONI DC. on *Lathyrus latifolius* (cult.). Sauk Co., Badger Village, November 16, 1949. Coll. G. H. Bridgman.

ERYSIPHE CICHORACEARUM DC. on *Asclepias tuberosa*. Dane Co., Madison, September 22, 1950. The same plant bore a heavy infection of *Microsphaera diffusa*. Also on *Cucurbita maxima*. Dane Co., Madison, September 18, 1950. On *Rudbeckia hirta*. Dane Co., Madison, September 8, 1950. Regularly infected with powdery mildew, but perithecia not hitherto noted in Wisconsin. *Rudbeckia laciniata* is likewise infected every season, but so far perithecia have not been observed.

CLAVICEPS PURPUREA (Fr.) Tul. Sclerotia on *Festuca ovina*. Dane Co., Madison, July 11, 1949.

PHYLLACHORA PUNCTA (Schw.) Orton on *Panicum perlongum*. Dane Co., Madison, September 15, 1950. Not listed on this host by Orton in his compilation of the graminicolous species of *Phyllachora*.

PUCCINIASTRUM PYROLAE (Pers.) Schroet. II on *Pyrola chlorantha*. Door Co., Bailey's Harbor, July 21, 1950.

MELAMPSORELLA CERASTII (Pers.) Schroet. II on *Stellaria longifolia*. Dane Co., Madison, August 22, 1950. The only previous Wisconsin records of this rust are of the aecial stage on *Abies* and *Picea*.

PUCCINIA VEXANS Farl. I on *Asclepias verticillata*. Green Co., Town of York near Daleyville, June 29, 1950. Arthur's Manual mentions only Nebraska and South Dakota as host localities.

PUCCINIA ASTERIS Duby on *Aster azureus*. Iowa Co. near Arena, August 1, 1950.

PHYLLOSTICTA NEBULOSA Sacc. on *Lychnis alba*. Door Co., Sturgeon Bay, September 1949. Coll. E. H. Varney. Seaver in his treatment of this species uses the name *P. pallida* Seym. & Earle. Ellis and Everhart distributed "*P. lychnidis* Fr." as No. 2839 of their North American Fungi, but in their North American Phyllostictas the following appears: "177. *Phyllosticta lychnidis* (Kz. & Schm.) *Sphaeria lychnidis* K. & S.—The specc. in Ell. & Ev. N. A. F. 2839 do not show any well-edevloped spores and are therefore doubtful." In 1912 *P. lychnidis* A. Bond. was described as occurring on *Lychnis chalcedonica* in Russia but, judging from the description, it does not differ significantly from *P. nebulosa* Sacc., except in having somewhat wider spores. In my opinion the Phyllostictas having this general range of spore size on Caryophyllaceae are probably all the same thing. So provisionally, I continue to use Saccardo's early name, since the description seems adequate.

PHYLLOSTICTA SICCATA H. C. Greene on *Solidago nemoralis*. Green Co., Sect. 1, Town of Sylvester, August 17, 1950. Described on *Solidago serotina*. This is the only collection since the type.

"PHYLLOSTICTA HELIANTHI Ell. & Ev." on *Helianthus rigidus*. Dane Co., Madison (Summit), June 27, 1949. I have already discussed (Farlowia 1: 572. 1944) a similar form on *Helianthus strumosus*. It is possible that *P. helianthi* is a nomen nudum, and also that it is the conidial stage of *Rosenscheldia heliopsidis* (Schw.) Theiss. & Syd., previously reported on *H. rigidus* in Wisconsin.

SELENOPHOMA EVERHARTII (Sacc. & Syd.) Sprague & Johns. on *Agropyron repens*. Dane Co., Madison, July 19, 1949.

ASCOCHYTA GRAMINICOLA Sacc. on *Elymus virginicus*. Dane Co. near Verona, August 1, 1949. The conidia are mostly about 12-14 x 3.5-4μ. It seems likely that this is the same thing that Tehon & Daniels (Mycologia 19: 124. 1927) described as *Ascochyta elymi*, differentiating it on the basis of pycnidial walls said to be thinner than those of *A. graminicola*. Sprague & Johnson (Mycologia 42: 530. 1950) substitute the name *A. sorghi* Sacc. for the well-known *A. graminicola*.

ASCOCHYTA AQUILEGIAE (Rabh.) v. Hoehn. on *Aquilegia* sp. (cult.). Dane Co., Madison, July 12, 1950. Davis (Trans. Wis. Acad. Sci. 26: 253. 1931) reported what he considered to be a microconidial state of this species, collected on *Aquilegia canadensis* near Sturgeon Bay, Door Co. von Hoehnel (Ann. Mycol. 3: 406. 1905) gives a rather complete discussion of this species which Saccardo evidently regards as being a later homonym for *Ascochyta aquilegiae* (Roum. & Pat.) Sacc. The conidia in the Madison specimen are mostly 10-12 x 2-3.5μ, the flesh-colored pycnidia 100μ diam. or more. The orbicular zonate lesions are of the type frequently produced by *Ascochyta*.

ASCOCHYTA COMPOSITARUM J. J. Davis on *Solidago gigantea* var. *leio-*

phylla (*S. serotina*). Dane Co., Madison, August 6, 1949. In the Wisconsin Herbarium there are numerous specimens filed under this name, nearly all collected by Davis. At one time Davis set apart a small-spored variety on *Helianthus*, but later placed it with the species. Although host response is diverse, conidial morphology in the larger-spored specimens is quite constant. In the current collection the lesion is more sharply defined than those in an earlier collection on *Solidago altissima*.

ASCOCHYTA RUDBECKIAE (Ell. & Ev.) Greene (*Phyllosticta rudbeckiae* Ell. & Ev.) on *Helianthus strumosus*. Green Co., New Glarus, August 14, 1950 and at Madison, August 23. The lesions and the superficial arrangement of the pycnidia on them, particularly in the Madison specimen, are exceedingly similar to the development of the fungus on *Rudbeckia laciniata*. The conidia run slightly smaller, and very few are septate, but it would scarcely be possible to clearly differentiate the form on *Helianthus* from that on *Rudbeckia*. From a comparison of specimens it does not appear that this is the same as the small-spoted *Ascochyta* on *Helianthus strumosus* which Davis once set aside as var. *parva* of his *A. compositarum*.

DARLUCA FILUM (Biv.) Cast. on *Puccinia eatoniae* Arth. II on *Sphenopholis intermedia* (*pallens*). Dane Co., Madison, July 26, 1949. On *Puccinia caricis* (Schum.) Schroet. II on *Carex stricta*. Dane Co., Madison, July 22, 1948. On *Uromyces lespedezae-procumbentis* (Schw.) Curt. III on *Lespedeza capitata*. Dane Co., Madison, September 24, 1949. Not common on *telia*. On *Uromyces verruculosus* Schroet. II on *Lychnis alba*. Door Co., Sturgeon Bay, September 1949. Coll. E. H. Varney.

STAGONOSPORA BAPTISIAE (Ell. & Ev.) Davis on *Lathyrus japonicus* var. *glaber* (*L. maritimus*). Sheboygan Co., Lake Michigan beach near Oostburg, October 9, 1949. Microscopically, practically identical with the specimens on *Baptisia*. The lesions are variable. Frequently the pycnidia occur sparsely on small, angled, sunken, brownish spots with darker elevated margins. In other instances the lesions are of indefinite extent and pale brown, with many pycnidia gregarious on them.

STAGONOSPORA ZONATA J. J. Davis on *Asclepias phytolaccoides*. Dane Co., Madison, September 7, 1950. The conidia here have a faintly smoky tinge and only a few have more than one septum. Nevertheless, the entirely characteristic lesions indicate that the collection should be referred to this highly variable species.

STAGONOSPORA CONVOLVULI Dearn. & House on *Convolvulus spithamaeus*. Green Co., Albany, August 8, 1950. Placed here because the pycnidia are well-formed. There seems little question that there is an intergrading series between *Septogloeum convolvuli* Ell. & Ev. and this species. *Septoria calystegiae* West. seems also to be a closely related form.

SEPTORIA NEMATOSPORA J. J. Davis on *Carex bromoides*. Iowa Co., Canyon Park near Dodgeville, June 11, 1950. Also noted on a phanerogamic specimen of the same host, collected by F. J. Hermann near Plainville, Adams Co., June 13, 1937.

SEPTORIA MELANDRII Pass. on *Lychnis dioica*. Dane Co., Madison, June 20, 1950.

SEPTORIA RHOINA B. & C. on *Rhus radicans*. Door Co., Gill's Rock, July 1950. Det. E. H. Varney.

SEPTORIA ATROPURPUREA Peck on *Solidago uliginosa*. Jackson Co. near Pray, August 16, 1950. The lesions are reminiscent of those usually produced by *Septoria solidaginicola* Peck, but the large pycnidia and long, thick spores are not those of the latter species. Also on *Aster cordifolius*. Sauk Co., Ferry Bluff, September 6, 1950.

HAINESIA LYTHRI (Desm.) Hoehn. on *Rosa* sp. Dane Co., Madison, August 25, 1945. The host is a formerly cultivated species which has escaped and become established.

COLLETOTRICHUM GRAMINICOLA (Ces.) Wils. on *Ammophila breviligulata*. Sheboygan Co., Lake Michigan beach near Oostburg, October 9, 1950.

COLLETOTRICHUM TRIFOLII Bain. & Essary on *Melilotus alba*. Dane Co., Madison, September 25, 1947. Also on *Medicago sativa* at Madison, October 13, 1950. Both coll. & det. by F. R. Jones.

COLLETOTRICHUM SOLITARIUM Ell. & Barth. on *Solidago missouriensis* var. *fasciculata*. Dane Co. near Springfield Corners, August 1, 1950. On this host the acervuli are more than usually numerous on the individual spots, which are sordid brown and indeterminate.

PHLEOSPORA ANEMONES Ell. & Kell. on *Anemone quinquefolia*. Door Co., Sturgeon Bay, July 9, 1950. Coll. E. H. Varney. The lesions are highly characteristic, although but few spores were found.

PASSALORA FASCICULATA (C. & E.) Earle on *Euphorbia preslii*. Dane Co., Madison, June 21, 1944.

SCOLECOTRICHUM GRAMINIS Fckl. on *Glyceria canadensis*. Jackson Co. near Pray, August 16, 1950.

HELMINTHOSPORIUM SATIVUM Pamm., King & Bakke on *Panicum implicatum*. Dane Co., Madison, August 8, 1949. Previously collected on *Panicum capillare* in Wisconsin.

CERCOSPORELLA BRASSICAE (Fautr. & Roum.) Hoehn. on *Sisymbrium officinale*. Jefferson Co., Faville Grove, June 29, 1949.

CERCOSPORELLA NIVEA Ell. & Barth. on *Solidago sciaphila*. Sauk Co., Parfrey's Glen, August 24, 1950.

CERCOSPORA HYDROPIPERIS (Thum.) Speg. on *Polygonum punctatum*. Dane Co., Madison, August 29, 1949.

CERCOSPORA POLYGONACEA Ell. & Ev. on *Polygonum scandens*. Dane Co., Madison, August 24, 1949.

CERCOSPORA BARBAREAE (Sacc.) Chupp on *Arabis canadensis*. Green Co., Pine Bluff near Brodhead, August 4, 1950. Det. Chas. Chupp.

CERCOSPORA VIOLAE Sacc. on *Viola selkirkii*. Sauk Co., Parfrey's Glen, August 24, 1950.

CERCOSPORA CLAVATA (Ger.) Cke. on *Asclepias purpurascens*. Dane Co., Madison, August 11, 1950.

CERCOSPORA DIFFUSA Ell. & Ev. on *Physalis subglabrata*. Green Co., Sect. 1, Town of Sylvester, August 17, 1950.

TUBERCULINA PERSICINA (Ditm.) Sacc. on *Puccinia angustata* Peck I on *Lycopus uniflorus*. Tower Hill State Park, Iowa Co. near Spring Green, June 24, 1949. Also on *Puccinia physalidis* Peck on *Physalis heterophylla*. Dane Co., Madison, July 30, 1950. This is the first occasion on which I have encountered this parasite, ordinarily found on the aecia of long-cycle rusts, on the telia of a microcyclic species.

ADDITIONAL SPECIES

The fungi mentioned have not been previously reported as occurring in Wisconsin.

VENTURIA CASSANDRAE Peck on *Andromeda glaucophylla*. Door Co., near Sturgeon Bay, July [illegible], 1950. Coll. & det. E. H. Varney.

PYRENOPHORA SECALIS Whitehead & Dickson on *Secale cereale*. Dane Co., Madison, May 1, 1948. Collected at various other stations in southern Wisconsin in the same month. This species has a parasitic *Helminthosporium* stage which, according to Whitehead and Dickson, has not previously been described.

ELSINOË AMPELINA (DeBary) Jenkins on *Vitis* sp. (*Sphaceloma ampelinum* DeBary). The spot anthracnose of grape is cited for Wisconsin by Jenkins and Bitancourt (Pl. Dis. Rep. 31: 114. 1947) on the basis of a state report, as shown by a card in the Plant Disease Survey file (Jenkins—personal communication), but there is no specimen in the Herbarium of the Division of Mycology and Disease Survey.

HYPODERMELLA MIRABILIS Darker on *Abies balsamea*. Price Co., Prentice, July 28, 1919. Coll. J. J. Davis. Not fully mature, but placed here because of the distinctive biseriate pycnidial pattern which Darker considers as diagnostic in the field for this species.

HERPOBASIDIUM FILICINUM (Rostr.) Lind on *Dryopteris Linnaeana*. Door Co., near Sturgeon Bay, July 8, 1950. Coll. & det. E. H. Varney. There was also an incorrectly determined specimen of the same fungus on the same host in the Wisconsin Herbarium, collected by L. S. Cheney at Devils Lake, Sauk Co., July 2, 1904. The latter would appear to be the earliest collected North American specimen of the fungus of which there is record.

MILESIA MARGINALIS Faull & Wats. II on *Dryopteris marginalis*. Door Co., near Sturgeon Bay, May 21, 1950. Coll. & det. E. H. Varney. It is possible that aecia on *Abies balsamea*, collected at the same time and in the same vicinity, are also of this species.

UROMYCES VERRUCULOSUS Schreet. II on *Lychnis alba*. Door Co., Sturgeon Bay, September 1949. Coll. & det. E. H. Varney. The range as given

in Arthur's Manual is the southern peninsula of Michigan to southern Indiana, and a station on Long Island; also in Europe. Only uredia have been reported from North America.

CERATOBASIDIUM ANCEPS (Bres. & Syd.) Jacks. is the new name applied by H. S. Jackson to replace *Corticium anceps* (Bres. & Syd.) Gregor, the sclerotial state of which is *Sclerotium deciduum* J. J. Davis. In my notes XIV (Amer. Midl. Nat. 44: 630) I listed the Wisconsin hosts of this fungus, using the name *Corticium anceps*. Jackson has examined all the specimens from Wisconsin, totalling 47 collections on 17 hosts. He was able to demonstrate basidia in 17 collections on 9 hosts as follows: *Adiantum pedatum*, *Onoclea sensibilis*, *Pteretis nodulosa* (*Onoclea struthiopteris*), *Pteridium aquilinum* var. *latiusculum*, *Aralia nudicaulis*, *Diervilla lonicera*, *Hydrophyllum virginianum*, *Solidago serotina*, and *Steironema ciliatum*.

Phyllosticta pennsylvanica sp. nov.

Maculis angulosis vel rotundatis, 1-3 mm. diam., pallido-brunneis vel albidis, marginibus angustis, brunneo-purpureis; pycnidiis epiphyllis, nigris, subglobosis, 75-125μ diam. ca. gregariis vel sparsis; conidiis ovalibus vel ovatis, hyalinis, granulosis, 5-7 x 7-10μ.

Spots angled or rounded, 1-3 mm. diam., pale brown or whitish, margins narrow, brownish-purple; pycnidia epiphyllous, black, subglobose, approx. 75-125μ diam., gregarious or scattered; conidia oval or ovoid, hyaline, granular, 5-7 x 7-10μ.

On living leaves of *Prunus pennsylvanica*. Devils Lake, Sauk County, Wisconsin, U. S. A., October 9, 1949. Coll. R. Raabe.

Some of the smaller spots show no trace of brown, having merely the white center bounded by a narrow purplish margin. The larger spots, however, are palest in the center and brownish in the outer portion, with the whole enclosed by the purplish margin. Many species of *Phyllosticta* on *Prunus* have been described, some of the earlier ones hardly adequately. In spore size *Phyllosticta congesta* Heald & Wolf seems closest to *P. pennsylvanica*, but the type of spots and the arrangement of the pycnidia on them seem to rule it out in this case. Interestingly enough, a specimen of what appears to be authentic *P. congesta* was collected on *Prunus pennsylvanica* at the same station in 1921 by J. J. Davis.

Phyllosticta wulfeniae sp. nov.

Maculis rotundatis, variis, confluentibus interdum, cinereis vel pallido-brunneis, tenuibus, marginibus angustis, elevatis, fuscis; pycnidiis epiphyllis, gregariis, subglobosis, fumoso-brunneis, 100-175μ diam.; conidiis hyalinis, numerosis, parvis, cylindraceis, brevibus, 4-6 x 2-2.5μ.

Spots rounded, somewhat variable in size and shape, sometimes confluent, cinereous or pale brown, thin, margin narrow, elevated, fuscous; pycnidia epiphyllous, gregarious, subglobose, sooty-brown, 100-175μ diam.; conidia hyaline, numerous, small, short-cylindric, 4-6 x 2-2.5μ.

On living leaves of *Wulfenia* (*Synthyris; Besseya*) *bullii*. Green County near Brodhead, Wisconsin, U. S. A., August 8, 1950.

This is not similar to *Phyllosticta digitalis* Bell., judging from specimens in the University of Wisconsin Herbarium, either in its effect upon the host, in the shape or definiteness of the lesions, or in the arrangement of the pycnidia on the lesions. Also the conidia are somewhat shorter. The conspicuous spots run from quite small to fairly large, the smallest being almost circular in outline.

Phyllosticta madisonensis nom. nov.

This name is offered to replace *Phyllosticta solidaginicola* H. C. Greene (Farlowia 1: 573. 1944) which I have discovered is a later homonym of *P. solidaginicola* Tehon & Daniels. Tehon has examined my type specimen and informs me that it appears to be distinct from his material. So far collected only in the Madison vicinity.

Phyllosticta favillensis sp. nov.

Maculis magnis, irregularibus, conspicuis, brunneis, marginibus angustis, fuscis, pycnidiis amphigenis, sparsis vel gregariis, nigris, subglobosis, 125-175μ diam. ca.; conidiis hyalinis, cylindraceis, 6-10 x 3-4μ.

Spots large, irregular, conspicuous, brown, with narrow fuscous margins; pycnidia amphigenous, scattered or gregarious, black, subglobose, approx. 125-175μ diam.; conidia hyaline, cylindric, 6-10 x 3-4μ.

On living leaves of *Silphium integrifolium*. Faville Prairie, Sect. 20, Town of Milford, Jefferson County, Wisconsin, U. S. A., August 4, 1949.

The spots are mostly marginal and somewhat elongate, sometimes involving as much as a fourth of the leaf. The conidia are larger than those of any other *Phyllosticta* that I have encountered on this type of lesion on Compositae.

Ascochyta cypripedii sp. nov.

Maculis angustis, elongatis, plerumque in apicibus, brunneis; marginibus angustis, fuscis; pycnidiis sparsis vel gregariis, epiphyllis, subglobosis, flavido-brunneis, plerumque 100-500μ diam.; conidiis hyalinis, guttulatis frequenter, obtusis, 6-8 x 3-3.5μ.

Lesions narrow, elongate, mostly including leaf tip, brownish with narrow dark brown border; pycnidia scattered or gregarious, epiphyllous, subglobose, yellowish-brown, mostly about 100-150μ diam.; conidia hyaline, frequently guttulate, ends obtuse, 6-8 x 3-3.5μ.

On living leaves of *Cypripedium candidum*. Madison, Dane County, Wisconsin, U. S. A., July 16, 1950.

Less than half the conidia examined show a septum. There seem to be no other reports of *Ascochyta* on *Cypripedium*.

Stagonospora spiculisperma sp. nov.

Maculis elongatis, pallido-flavis, marginibus latis, brunneis, 1.5-4 mm. longis, confluentibus interdum; pycnidiis epiphyllis, paucis fere, multis confer-

tisque interdum, subepidermidibus, planis et distortis varie, nigris, magnis, 150-250μ diam., 200μ pierumque; conidiis hyalinis, basibus truncatis, apicibus tenuibus et curvis leviter, 35-50 x 4-4.5μ, 4-7-septatis.

Spots elongate, pale straw-colored, with rather wide diffuse brownish margins, 1.5-4 mm. long, sometimes confluent; pycnidia epiphyllous, usually few, but sometimes many and crowded, subepidermal, variously flattened and disotrted, black, large, 150-250μ diam., mostly about 200μ; conidia hyaline, truncate at base, tapering to a slender tip which is somewhat curved, 35-50 x 4-4.5μ, 4-7-septate.

On living leaves of *Stipa spartea*. Iowa County near Arena, Wisconsin, U. S. A., August 1, 1950. Also collected in Green County near Brodhead, Wisconsin, August 8, 1950.

The distortion of the pycnidia results from the strong ribbing of the narrow leaves of this xerophyte. The conidia are widest at about the mid-point, being slightly narrower at the base and much narrower at the tip.

STAGONOSPORA SIMPLICIOR Sacc. & Berl. f. ANDROPOGONIS Sacc. on *Andropogon furcatus*. Dane Co., Madison, August 28, 1943; Dane Co. near Sauk City, August 1, 1945; Columbia Co., Black Hawk's Lookout near Prairie du Sac, August 20, 1948; Sauk Co., Cactus Bluff, Town of Prairie du Sac, September 18, 1948. On *Sorghastrum nutans*. Dane Co., Madison, August 20, 1943; Green Co., Sept. 1, Town of Sylvester, July 6, 1947; Green Co., Sect. 36, Town of Mt. Pleasant, August 7, 1948. On *Panicum implicatum*. Jefferson Co., Faville Prairie near Lake Mills, June 30, 1948. On *Panicum latifolium*. Sauk Co., Devils Lake, August 16, 1949. On *Panicum leibergii*. Dane Co. near Belleville, August 12, 1949. On *Panicum scribnerianum*. Dane Co., Madison, August 16, 1943; Dane Co. near Sauk City, September 5, 1945; St. Croix Co. near Hudson, August 22, 1946. In some cases more than one specimen has been collected at a single station, notably Madison. The lesions vary considerably according to hosts, being best defined as sharply delimited spots on *Panicum leibergii* and *P. scribnerianum*. On *Andropogon furcatus* they are only slightly less well-marked, but on *Sorghastrum nutans* considerably so. On *Panicum latifolium* the lesions vary from small, brown fusoid areas on living leaves to cases where the entire leaf is brown and dead, while on *Panicum implicatum* the affected leaves were dead. The pycnidia are prominent, usually amphigenous, mostly over 100μ diam., black and from one or few to many per lesion, depending on the size of the lesion. The conidia are quite regularly 3-septate, conspicuously guttulate, and cylindric. On *Panicum* they run slightly smaller, mostly about 8-10 x 25-35μ, while on *Andropogon* and *Sorghastrum* they are about 10-12 x 30-35μ. This seems to be quite a characteristic fungus, and over the years I have accumulated enough specimens so that I feel reasonably sure I am dealing with an entity. A somewhat similar form was collected on *Phragmites communis* (Farlowia 1: 575. 1944), the host species from which *Stagonospora simplicior* was described. On *Phragmites* the fungus appears saprophytic and it seems questionable whether it is the same as the organism on *Panicum*, *Andropogon* and *Sorghastrum*.

Stagonospora thaspii (Ell. & Ev.) comb. nov.

(*Ascochyta thaspii* Ell. & Ev., Jour. Mycol. 5: 148. 1889.)

I have long suspected that this species, with spores 18-30 x 4-8μ, as originally described, should be referred to *Stagonospora*. A specimen on *Oxypolis rigidior*, collected at Madison in September 1949 confirms that view. The spores are mostly about 25-35 x 6-8μ and many of them are 2-septate. A specimen on *Zizia aptera*, collected in 1946, also has some 2-septate spores. *Ascochyta thaspii* has been reported on a number of Umbelliferae in Wisconsin. I believe that all these specimens represent a single rather variable species and that in time other multiseptate examples will be collected.

Stagonospora verbenae sp. nov.

Maculis parvis, albis, 0.5-0.75 mm. diam., aggregatis in maculis amplioribus fusco-purpureis; pycnidiis epiphyllis, globosis, nigris, muris tenuibus, 125-175μ diam. ca.; conidiis rectis vel curvis leviter vel flexuosis aliquantum, apicibus obtusatis, subcylindraceis, hyalinis, guttulatis fortiter, 12-18 x 3μ, 1-2-septatis plerumque, 3-septatis interdum.

Spots small, white, 0.5-0.75 mm. diam., clustered in larger dark purple areas; pycnidia epiphyllous globose, black, thin-walled, approx. 125-175μ diam.; spores straight or slightly curved or somewhat flexuous, ends obtuse, subcylindric, hyaline, strongly guttulate, 12-18 x 3μ, mostly 1-2-septate, occasionally 3-septate.

On living leaves of *Verbena stricta*. Madison, Dane County, Wisconsin, U. S. A., August 8, 1949.

Not all the small white spots bear pycnidia and those that do have but a single pycnidium per spot. Although the individual spots are very small, the lesions are quite conspicuous because of the dark purple matrix about the clusters of spots. Most of the leaves of the specimen also bear *Cercospora verbenicola* Ell. & Ev. The guttulation of the spores is so pronounced as to interfere somewhat with the observation of the septa. It seems possible that this may be a more mature state of an *Ascochyta* which I collected several years ago on *Verbena stricta* in the same vicinity, and at the time referred to *Ascochyta verbenae* Siemaszko.

Septoria anychiae sp. nov.

Maculis nullis, pycnidiis gregariis, amphigenis, globosis, subrostratis, nigris, parvis, 40-65μ diam. ca.; conidiis hyalinis, continuis, rectis vel curvis leviter, 12-23 x 1μ, plerumque 20μ.

Spots none; pycnidia gregarious, amphigenous, globose, subrostrate, blackish, small, approx. 40-65μ diam.; conidia hyaline, continuous, straight or slightly curved, 12-23 x 1μ, mostly 20μ long.

On lower leaves of *Anychia canadensis*. Pine Bluff, 2 miles southwest of Brodhead, Green County, Wisconsin, U. S. A., August 4, 1950.

The fungus is almost confined to the lower pair (cotyledonary?) of stem leaves, which have been entirely killed back on all the infected plants. The only other species of *Septoria* occurring on a species of the Illecebraceae, so

far as I have been able to determine, is *Septoria scleranthi* Desm., a much coarser form.

Septoria taraxaci Hollos on *Taraxacum officinale*. Dane Co., Madison, October 10, 1949. Coll. R. Raabe.

COLLETOTRICHUM DESTRUCTIVUM O'Gara on *Medicago sativa*. Dane Co., Madison, Summer 1950. Coll. & det. F. R. Jones.

Marssonina gloeodes (H. C. Greene) comb. nov.

By an unfortunate error published as *Marsonia gloeodes* (Trans. Wis. Acad. Sci. 38: 231. 1946).

MARSSONINA QUERCINA (Wint.) Lentz (Mycologia 42: 259. 1950) is the name applied by Lentz to the fungus occurring on the black oak group which appears in Wisconsin lists as *Gloeosporium septorioides* Sacc. Davis reported this organism on *Quercus alba*, but stated that the collection was doubtfully distinct from *Marssonina martini* (Sacc. & Ell.) Magn.

RAMULARIA ANAGALLIDIS Lindr. on *Veronica "spicata"* (cult.). Dane Co., Madison, August 6, 1950. This seems distinct from *Ovularia veronicae* (Fckl.) Sacc. (*Ramularia veronicae* Fckl.), being a decidedly more delicate form, with most of the conidia 1-septate.

SYNTHETOSPORA ELECTA Morg. on *Paxinus* sp. Dane Co., Madison, September 25, 1950. Coll. & det. E. H. Varney. Specific determination of the host is not feasible because of the distortion produced by the parasite. A curious and interesting fungus. The first Wisconsin record of a parasitic representative of the Staurosporae.

CURVULARIA LUNATA (Wakker) Boedijn on *Polygala verticillata*. Dane Co., Madison, July 31, 1950. Although the stems are infected at ground line in most plants, there is no continuity between this lesion and those which may occur higher up on the stem, leaves, or inflorescence. A host plant thus may, and usually does, have several apparently separate infections. Boedijn set up the genus *Curvularia* to include a related series of fungi having few-celled, mostly strongly curved, conidia of the *Helminthisporium-Acrothecium* type (Bull. Jard. Bot. Biutenzorg. 3rd ser. 13: 123. 1933). It seems worthwhile to give the following rather full notes on the Wisconsin specimen: Conidiophores in dense groups on stems, leaves and inflorescences, frequently girdling stems at soil line, black in mass, individually, by transmitted light, pale brown above, but often darker and thicker in the lower third, 1-3 times geniculate, apices inflated or denticulate, 65-105 x 4-6μ, 3-6-septate; conidia 4-celled, clear gray-brown, curved, penultimate cell typically strongly convex on one side and markedly larger than any of the other three cells, also usually thicker-walled and somewhat deeper brown, basal cell conical with noticeable spore scar at narrow end, 25-35 x 12-14μ.

CERCOSPORA MACCLATCHIEANA Sacc. & Syd. on *Ceanothus ovatus*. Dane Co., Primrose Prairie, Town of Perry, August 12, 1949. There appear to be two species of *Cercospora* on both of the Wisconsin species of *Ceanothus*. According to Chupp, these are 1) *C. ceanothi* Kell. & Sw. which has small

stromata and fascicles, mostly dense; conidiophores very pale-colored, non-septate, 2-4 x 5-50μ conidia subhyaline to very pale-colored, obclavate, 2-4 x 20-100μ, and 2) *C. macclatchieana* (syn. *C. fuliginosa* Ell. & Ev.) which is non-fasciculate with the conidiophores as branches from procumbent threads, plainly septate, 4-6.5 x 10-75μ; conidia obclavate-cylindric (rarely clavate), 5-7.5 x 40-130μ. The conidia seem to me to be the most clearly differentiated structures. Davis (Trans. Wis. Acad. Sci. 18 (1): 86. 1915) regarded *C. macclatchieana* as being but a later season development of *C. ceanothi*. As I have stated, the conidia are so widely divergent in shape, size and color (those of *C. macclatchieana* are much darker) that I do not think that Davis' view is justified. Chupp further points out that he does not think that *C. macclatchieana* is a good species of *Cercospora*, but more likely belongs with *Helminthosporium*, because its conidia typically have thick walls. Since it seems totally unlike the graminicolous *Helminthosporiums* with which I am familiar, and has not yet, so far as I am aware, been transferred to that genus, I think it best for purposes of present record to report it as a *Cercospora*. In addition to the specimen cited above there are several other collections of *C. macclatchieana* in the Wisconsin Herbarium, most of them on *Ceanothus americanus*.

ALTERNARIA RADICINA Meier, Drechsler & Reddy on *Daucus carota* var. *sativa*. Kenosha Co., Kenosha, September 30, 1949. Coll. R. Raabe. In the specimen seen by me the fungus is on the petioles and appears parasitic. The authors state (Phytopath. 12: 166. 1922) "The appearance of this disease on the foliage when it occurs as the result of artificial infection is similar to that produced by *Macrosporium carotae* Ell. & Langlois, a distinct species and obligate parasite, producing in nature a widely distributed foliage blight of actively growing carrot plants. *Alternaria radicina* may perhaps best be regarded as a facultative parasite of undoubted vigor affecting mature tissues, particularly those of the more or less bruised or wounded roots while being harvested or undergoing storage." A study of the authors' figures leaves no doubt as to the identity of the Wisconsin specimen.

XENOGLOEA ERIOPHORI (Bres.) Syd. is the name properly applied to the fungus occurring in Wisconsin on *Scirpus atrovirens* and cited in previous lists as *Kriegeria eriophori* Bres. As the Sydows pointed out (Ann. Mycol. 17: 44. 1919), *Kriegeria* is untenable because of prior usage.

STILBUM TOMENTOSUM Schrad. ex Fr. on *Hemitrichia vesparium*. Also collected at the same time on *Trichia persimilis*. Dane Co., Madison, October 5, 1950. Det. M. P. Backus.

Uniparental Miracidia of Schistosomatium douthitti and Their Progeny (Trematoda, Schistosomatidae)*

Robert B. Short

Department of Zoology, Florida State University, Tallahassee

In a paper to be published elsewhere I show that females of *Schistosomatium douthitti* mature sexually in definitive hosts (mice) in the absence of males; that these females lay eggs and that many such eggs develop parthenogenetically, giving rise to uniparental miracidia. It is pointed out that in unisexual infections with female *S. douthitti* development of miracidia is not sporadic and unpredictable, but is of regular occurrence.

During the experiments mentioned above, examinations were made of the eggs in fresh tissues (intestine, liver, spleen and lung) removed from hosts carrying ♀ and ♂-♀ infections. These examinations revealed no differences between the uniparental miracidia and those from biparental infections. However, it was thought desirable to make further studies on miracidia from both sources to detect, if possible, any abnormalities in the uniparental miracidia which might have resulted from lack of fertilization of the eggs from which they developed. It was also considered of interest to determine whether miracidia derived from unfertilized eggs could penetrate snails and give rise to cercaria-producing infections. That uniparental miracidia are infective for snails has been demonstrated, and an abstract (Short, 1948) gives some results of these experiments.

The present work is concerned with studies on the morphology, behavior and size of uniparental miracidia and a comparison of such miracidia with those from biparental infections. This paper also presents, in more detail than given previously, results of exposing snails to uniparental miracidia and an account of the progeny thus derived.

All my unpublished results referred to in the present paper are containd in a paper entitled "*Sex Studies on Schistosomatium douthitti* (Cort, 1914) Price, 1931 (Trematoda: Schistosomatidae)." (Amer. Midland Naturalist, in press.)

Materials and Methods

The present experiments are a continuation of the unpublished work referred to above and the materials and methods employed are the same. However, to the materials and methods given in that paper should be added the following, which also pertain to the present work.

---

* Contribution from the Department of Zoology, University of Michigan. This paper is a portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

I wish to express my sincere gratitude to Professor George R. La Rue under whose direction this work was done.

All mammalian hosts used in the experiments herein reported were laboratory-reared deer mice (*Peromyscus maniculatus*) which were known to be free from schistosome infection before experimental exposure. These mice were kindly supplied by the Laboratory of Vertebrate Biology of the University of Michigan.

Measurements of miracidia and cercariae were made with a compound microscope (10x oc. and 3 mm. obj.) on specimens in the fluid in which they were killed. In order to avoid distortion of specimens by coverslip pressure, the coverslips were supported by small pieces of glass or paper strips. Miracidia to be measured were placed singly in small drops of water on glass slides and killed by heat from an alcohol lamp. Cercarial measurements were made on specimens (ventral or dorsal surface up) which had been fixed by pouring the water containing them into about twice the volume of steaming hot 10% formalin.

UNIPARENTAL MIRACIDIA

As indicated above, microscopic examinations were made of many miracidia within eggs in fresh tissues of mice harboring unisexual infections, and such miracidia appeared entirely normal in structure and activity. In addition to these studies, observations were made on uniparental miracidia which had hatched from eggs in liver tissue and feces, and these specimens were compared with miracidia from biparental infections in behavior, morphology and size.

No difference in behavior of the two types of miracidia was noted. The uniparental specimens readily hatched in side-arm flasks from eggs in feces and liver tissue and congregated in the side arm in the same manner as those from biparental infections. Uniparental miracidia also swam normally, and under the stereobinocular and compound microscopes could not be distinguished from miracidia from biparental infections either in action or general appearance.

Under the oil immersion objective, detailed examinations of miracidia from the two types of infections revealed no difference in structure. Practically all the morphological details described and pictured by Price (1931) were seen in specimens from both sources.

For a comparison of the size of miracidia from unisexual and ♂-♀ infections, measurements of length and width (greatest) were taken. The results of these studies, together with other pertinent data, are given in Table 1. Fifty miracidia from biparental and 60 from uniparental infections were used. Specimens of each type were derived from the liver and feces of two mice, one male, the other female. The two ♂-♀ infections used were especially favorable for this purpose, since in each there was a large majority of male worms. Thus it was guaranteed, insofar as possible, that the miracidia in these infections had developed from fertilized eggs. In mouse No. C-48 there were 99 males and two females, while in C-49 there were 62 males and five females.

From the data of Table 1 it can be seen that the miracidia from biparental infections were considerably larger than those from uniparental infections, with the ratio of length to width about the same for both types. By means of the standard error of the difference from both lengths and widths it can be demonsrated that this difference in size of the two groups of miracidia is statistically significant.

TABLE 1.—Measurements in microns of miracidia of *Schistosomatium douthitti* from biparental and uniparental infections*

Mouse no. and sex	Average length	Average width	Total measured	No. from liver	No. from feces
		Biparental Infections			
C-48 ♂	100.65 ± 1.37	64.96 ± 0.76	50	10	10
C-49 ♀				20	10
		Uniparental Infections			
B-90 ♂	81.79 ± 0.92	58.24 ± 0.63	60	10	10
B-103 ♀				20	20

* The standard errors of the means are given.

For the purpose of the above comparison between miracidia from ♀ and ♂-♀ infections, and in the remainder of this paper, all miracidia from ♂-♀ infections are assumed to have developed from fertilized eggs. However, it should be noted that this may not be true; for it seems entirely possible that some miracidia in ♂-♀ infections may develop parthenogenetically. This possibility is suggested by our knowledge of parthenogenetic development of eggs in unisexual infections, together with the finding that female worms in ♂-♀ infections are not always inseminated. As a matter of fact, sectioned material shows that even in females which have been inseminated there may be unfertilized uterine eggs (Short, unpublished). Furthermore, the fact that miracidia known to be uniparental appear entirely normal* makes it impossible to determine which, if any, of the miracidia in biparental infections are uniparental.

It seems probable, however, that the large majority of the miracidia, if not all of them, in ♂-♀ infections had developed from fertilized eggs, for an examination of stained whole mounts of females from many of these infections showed that practically all had been inseminated, even when males were less numerous than females.

The assumption that all miracidia in ♂-♀ infections had developed from fertilized eggs seems especially justified in case of the miracidia used for

* Although uniparental miracidia proved to be of smaller average size than those from ♂-♀ infections (presumably biparental), the size ranges of the two groups overlapped, and taken individually the two types of miracidia are indistinguishable.

measurements, since for each female worm there were many males. This assumption is supported also by the fact that each of the two groups of miracidia was rather homogeneous as far as size is concerned, and that one group was significantly larger than the other.

The results of the comparison of morphology and behavior of the two types of miracidia would not be affected even if a few of the miracidia examined from the ♂-♀ infections had been uniparental, for many specimens from various ♂-♀ infections were examined, and certainly most of these had developed from fertilized eggs.

INFECTION OF SNAILS WITH UNIPARENTAL MIRACIDIA

Natural biological interest suggested experiments to determine whether miracidia derived from unfertilized eggs could penetrate snails and give rise to infections which would result in the production of cercariae. For this purpose 373 young laboratory-reared snails (285 *Lymnaea palustris* and 88 *L. stagnalis*) were exposed to miracidia which had hatched in side-arm flasks from eggs in feces or liver tissue of 14 mice with unisexual infections. The *palustris* were about two to eight weeks old when exposed. No age records are available for the *stagnalis*, but they measured two to 12 mm. long at exposure. For hatching miracidia and exposing snails, water was obtained from Semaphore Spring (near Dexter, Michigan) and from a large aquarium containing well-aerated tap water. Some snails were exposed to one to five miracidia each in small glass cups but most of the exposures were made in finger bowls or stender dishes in which several snails were exposed *en masse* to many miracidia. One group of snails was exposed in an aquarium into which many hatched miracidia and mouse feces containing eggs were placed.

Observations on the behavior of some of these miracidia in the presence of snails were made with a stereobinocular. In their reaction to snails these miracidia and those from ♂-♀ infections (Short, unpublished) presented no noticeable difference. Some uniparental miracidia seemed definitely aware of the snails and in several instances were seen to strike the head, tentacles and foot of the snail as though they were attempting to penetrate. None, however, was seen in the act of penetration.

Of the 373 snails exposed, 307 (231 *palustris* and 76 *stagnalis*) survived for about six to seven weeks and were examined for emerging cercariae. Infections producing cercariae were realized in two of the *palustris* and three of the *stagnalis*, giving a percentage of infection of 1.6 based on the number of both species of snails which survived and were examined. Sixty-four of the snails, negative for cercariae, were dissected and no sign of infection was seen in them. The remaining negative specimens were examined for emerging cercariae until about eight weeks after exposure and then were discarded.

It is noticed that in only a very small proportion of the snails exposed to uniparental miracidia were cercaria-producing infections obtained. The percentage of infection (1.6) in this group of snails is considerably lower than the 12.6% which occurred when young laboratory-reared snails of comparable ages were exposed to single miracidia from ♂-♀ infections (Short, unpub-

lished). In view of the fact that in most instances each snail was exposed to several uniparental miracidia, the rate of infection seems especially low; for similar exposures of snails to several miracidia from ♂-♀ infections usually produce higher rates of infection than when single miracidia are used. The results therefore indicate that miracidia derived from unfertilized eggs are less able to cause cercaria-producing infections in snails than miracidia derived from fertilized eggs. It is not known whether this reduced ability of uniparental miracidia to cause infections results from a diminished power to penetrate snails or from a lowered ability to develop within the snail. Both factors may operate.

The infections in snails resulting from uniparental miracidia differed in no discernible way from the usual experimental infections produced in laboratory-reared snails by miracidia from ♂-♀ infections. Although the daily cercarial output from three of the snails (two *palustris* and one *stagnalis*) was rather small, from the other two, larger numbers of cercariae emerged, sometimes 200 to 300 per day from each snail.

The two infected *palustris* were fixed for future study 103 days after they were first found to be infected, and two of the *stagnalis* after 17 and 39 days respectively. These snails had been examined for cercariae repeatedly throughout their lives, and no indication was given that the infections were waning.

The remaining infected snail was examined for emerging cercariae for several days after it was first found positive and then it was neglected for about seven months. During this time it was in a jelly glass with pieces of maple leaves for food, and the water was changed only occasionally. After the seven month period under such conditions, the snail was again examined on six successive days and no cercariae were found. Upon dissection, sporocysts with a few small cercarial embryos were seen, but no cercariae. Some diffuse spots of pigment, apparently disintegrating eyespots, were observed in what appeared to be dead cercariae. The over-all appearance was that of a poor infection. However, I doubt that the general necrotic condition of this infection, with the lack of cercarial production, should necessarily be attributed to the fact that the infection had arisen from a uniparental miracidium. I believe, rather, that the prolonged unfavorable conditions under which the snail existed had a deleterious effect on the parasite, and it seems probable that any infection would have similarly suffered.

CERCARIAE DERIVED FROM UNIPARENTAL MIRACIDIA

With cercariae available from infections produced by uniparental miracidia, it was of much interest to determine whether such cercariae would be infective for mice, and, if so, what would be the sex of the resulting worms. Experiments to test the infectivity of these cercariae were successful, and worms of both sexes developed. These experiments will be described in some detail following a report of results of a study of some of these cercariae to determine whether they were normal in morphology, behavior and size. It is assumed in this study that cercariae other than those known to be de-

scended from uniparental miracidia were derived from miracidia which had developed from fertilized eggs. These cercariae, assumed to be progeny of biparental miracidia, are called normal.

Careful microscopical examinations of cercariae derived from uniparental miracidia revealed no difference between their structure and that of cercariae descended from miracidia from ♂-♀ infections or from the figures and description of cercariae of *S. douthitti* given by Price (1931).

The behavior of cercariae derived from uniparental miracidia was studied under a stereobinocular and compared with descriptions of cercariae of *S. douthitti* in the literature as well as with my own observations on the behavior of cercariae from naturally infected snails and from laboratory-reared snails experimentally infected with miracidia from ♂-♀ infections. With the exceptions mentioned below, the cercariae derived from uniparental miracidia behaved normally. They escaped from the snails in the evening soon after dark and the majority emerged within about an hour's time (Cort and Talbot, 1936; Penner, unpublished thesis). Their swimming movements and general actions corresponded with those reported by Cort (1915), Price (1931) and Cort and Talbot (1936). Soon after emerging from the snail they swam to the surface of the water and attached to the surface film, ventral side up with their tails hanging down approximately at right angles to the body. Cort and Talbot emphasized this habit of attaching to the surface film displayed by cercariae of *S. douthitti.*

Exceptions to normal behavior were noticed in cercariae from three of the fine snails infected with uniparental miracidia. Many, often the majority, of cercariae from these three snails were found not attached to the surface film, but on or near the bottom of the containers. In such instances most of the cercariae on the bottom were inactive or moving feebly and appeared exhausted or dead. The cercariae usually emerged at night and examinations were made at various times during the following morning and afternoon. At similar intervals after emergence from snails, most normal cercariae were usually found attached to the surface film.

During these studies the water in which the snails were living was changed daily and care was taken to rinse out cecariae which had emerged on the previous day. Sometimes snails were transferred to different containers on successive days so as to assure that all the cercariae present had emerged within the 24 hours previous to observation. In spite of these precautions, daily counts of the cercariae from three snails infected with uniparental miracidia revealed that the majority were consistently found at the bottom of the containers. It thus appears that the cercarial progeny from three uniparental miracidia had a reduced vitality and became exhausted before the normal time; and it is possible that a careful comparison with the life span of normal cercariae might have revealed that the cecariae from the remaining two snails infected with uniparental miracidia also had a shorter than normal free-living period.

Since uniparental miracidia were found to be smaller than those derived from ♂-♀ infections (presumably biparental), the question arose as to

whether the cercarial progeny of uniparental miracidia were likewise smaller than cercariae derived from miracidia developed from fertilized eggs. In an attempt to answer this question, cercariae from three groups of snails were measured: (1) laboratory-reared snails infected with uniparental miracidia, (2) laboratory-reared snails infected with miracidia from ♂-♀ infections, and (3) naturally infected snails. Measurements were taken of length and width of body, length and width of tail stem, length of furcae, length and width of head-organ, diameter of acetabulum, and distance of acetabulum to anterior end. The number and species of snails used for each type of infection and the number and sex of cercariae from each snail are presented in Table 2. The sex of the cercariae was determined by infecting mice. It will be noted that the cercariae from two snails with uniparental miracidial infections were grouped together, while those from each of the remaining snails were kept separate. It was hoped that a comparison of the measurements of cercariae from the various snails would reveal the existence of any differences in size which could be attributed to development from uniparental or biparental miracidia.

Taken as a group, the cercariae derived from uniparental miracidia were smaller than those from miracidia presumed to be biparental; but the results are not conclusive, and therefore only measurements of body-length are given in Table 2.* An examination of the body-lengths shows this tendency for cercariae from uniparental miracidia to be smaller than the others and it is interesting to note that the groups of cercariae showing a reduced vitality (from snails N-1, N-2 and G-1) had the smallest measurements. However, the size of cercariae from different laboratory-reared snails carrying the same type of infection is not sufficiently consistent to permit determination with certainty whether the variation in size between cercariae derived from different types infection resulted from the parentage of the miracidium, i. e. uniparental or biparental. The data indicate, rather, that variations in size of cercariae from different snails may have resulted largely from factors other than the type of miracidium. Some factors which may affect the size of cercariae (and possibly also their vitality) are: species of snail; size of snail; environmental conditions under which the snail grew, including type and amount of food, size of body of water, chemical content of water, etc.; age of infection in the snail; intensity of infection; and time elapsing since emergence of cercariae.

Since the various factors involved and the extent of their influence are not known, it is impossible from these data to determine to what degree cercariae derived from uniparental miracidia are normal in size. The results, however, suggest that such cercariae have a tendency to be smaller than normal

---

* Measurements of body-length of cercariae of *S. douthitti* made by Price (1931) and Penner (1942) are also presented in Table 2. It was thought that since these authors fixed their specimens in hot 10% formalin, as I did, my measurements of normal cercariae might be comparable to theirs. However, this is not true, for my specimens were consistently smaller than theirs.

specimens. Although my measurements of cercariae do not serve well the purpose intended, they show what great variations exist in size of cercariae of one species from different snail hosts, and they strongly indicate the need for further and more carefully controlled experiments designed to determine the degree of variation which exists among cercariae derived from presumably biparental miracidia, and what factors are responsible for this variation.

TABLE 2.—Comparison of body lengths in microns of cercariae of *Schistosomatium douthitti* from different snails infected with uniparental and presumably biparental miracidia*

Species of snail	No. of snail	Sex of cercariae	No. of cercariae measured	Mean body-length
Laboratory-reared Snails Infected with Uniparental Miracidia				
L. palustris	N-1	female		
L. palustris	N-2	male	20	150.9 ± 3.95
L. stagnalis	G-1	male	20	131.9 ± 1.65
L. stagnalis	C-2	male	20	177.2 ± 1.83
Laboratory-reared Snails Infected with Miracidia from Biparental Infections (presumably biparental miracidia)				
L. palustris	A-8	female	20	182.8 ± 1.39
L. palustris	A-10	female	20	175.4 ± 1.22
Naturally Infected Snails				
L. palustris	W-1	male	20	183.3 ± 2.79
L. palustris	W-6	male & female	20	184.4 ± 1.37
L. palustris	W-9	male & female	20	180.2 ± 1.86
Measurements of Price (1931)				
?			25	204 (186-240)
Measurements of Penner (1942)				
L. stagnalis			20	200 (188-240)
Stagnicola reflexa (Lymnaea reflexa)			20	195 (186-228)

* The standard errors of the means are given for my measurements; for Price's and Penner's measurements the ranges are given.

WORMS DERIVED FROM UNIPARENTAL MIRACIDIA

As indicated above, the cercariae derived from uniparental miracidia were infective for mice and gave rise to male and female worms. One to five mice were exposed to cercariae from each snail, and autopsy of each mouse revealed unisexual infections with apparently normal worms. All the worms resulting from the cercariae from one snail were females, while those from the four other snails were males. Thus it was demonstrated that cercariae from

all five snails were infective, and furthermore that each snail harbored a unisexual infection, the male to female ratio being 4:1. Mice were not infected with cercariae from more than one snail, so no ♂-♀ infections were produced with cercariae derived from uniparental miracidia.

A total of 27 female worms were recovered from two mice (infections of 41-44 and 60-70 days) exposed to cercariae from one snail, and 348 males from 12 mice (infections of 18 to 263 days) infected with cercariae from the four other snails. The percentage of worm recovery was calculated for both sexes and found to be 19.7 for the females and 28.1 for the males. These percentages were obtained from so few data that their significance may be questioned; but the fact that for both sexes the percentages are much smaller (slightly over one-half) than those obtained when normal cercariae were used (Short, unpublished), suggests that cercariae derived from uniparental miracidia are less infective than normal ones. This suggestion is in keeping with the observations that some of the cercariae derived from uniparental miracidia apparently had a reduced vitality.

With the exception of one mouse harboring male worms, all mice infected with cercariae derived from uniparental miracidia were killed and autopsied immediately. The distribution of the worms in these infections corresponded to the distribution of those in the unisexual infections of my main series (unpublished). The majority of females were recovered from the liver, while most of the males were found in the extra-hepatic portal system.

Specimens of both sexes were fixed (from 0.75% saline) in Bouin's solution, and stained whole mounts were prepared by the same method described in my unpublished paper. Measurements were taken of all unbroken female specimens, and of groups of males 41, 45 and 53 days old. The results of these measurements are given in Table 3, together with measurements of worms of comparable ages from the main series of unisexual infections (unpublished). The worms of the main series are assumed to be derived from fertilized eggs. From these data it is evident that both male and female worms derived from uniparental miracidia are smaller than those of comparable ages in the main unisexual series.*

The stained whole mounts of worms derived from uniparental miracidia when examined microscopically appeared entirely normal. Both males and females were sexually mature; the males had many spermatozoa in their seminal vesicles and the females held the usual numbers of eggs in their uteri. No spermatozoa were seen in the 22 female worms examined.

Microscopical studies were made of the eggs in fresh liver and intestinal tissue from the two mice infected with female worms. Miracidia and the various types of eggs usually encountered (Short, unpublished) were found;

* Worms from the main *unisexual* series are used for comparison because all the worms derived from uniparental miracidia were from unisexual infections. With females this is important because, for the ages of worms used, there is a difference in size of specimens from unisexual and ♂-♀ infections in the main series. With males, of course, it makes little difference whether the main unisexual or ♂-♀ series is used, for the sizes of worms in each are similar.

however, only very few miracidia and embryos were seen. The large majority of eggs in both mice were dead and degenerate. These findings differ from those in the main unisexual female series, where, in infections of similar ages, there were proportionately many more miracidia and fewer dead and degenerate eggs.

The miracidia in these infections with female worms derived from uniparental miracidia evidently developed from unfertilized eggs, for no males were present and no spermatozoa were found in the females examined. Thus, we have second generation parthenogenetic miracidia, i.e. miracidia which developed parthenogenetically from eggs produced by female worms which themselves were derived from parthenogenetically devloped eggs. Because of the scarcity of material, no attempts were made to infect snails with these second generation parthenogenetic miracidia.

TABLE 3.—Comparison of lengths, in millimeters, of *Schistosomatium douthitti* derived from uniparental miracidia with lengths of worms derived from miracidia presumed to be biparental (i. e. miracidia from ♂-♀ infections)*

Worms derived from uniparental miracidia				
Age (days)	No. worms measured	Average length	No. mice used	
		Females		
41-44	8	1.759±.040	1	
60-70	7	1.743±.031	1	
		Males		
41	22	3.636±.095	2	
45	12	3.434±.199	1	
53	29	3.542±.098	2	
Worms derived from biparental miracidia				
Age (days)	No. worms measured	Average length	No. mice used	*t*
		Females		
40	24	2.047±.049	2	4.55
62	65	2.004±.040	4	5.16
		Males		
40	30	4.253±.081	1	4.94
60	29	4.306±.076	1	6.16

* All worms are from unisexual infections. The standard errors of the means are given, and also the *t* values for the differences between means of worms of comparable ages from the two series.

DISCUSSION

In interesting crossing experiments of Vogel (1941) between males of one species of *Schistosoma* and females of another, mice and hamsters were infected with five different combinations. In every cross the females de-

veloped to sexual maturity and produced eggs. However, only in infections with *japonicum* ♂♂ x *mansoni* ♀♀ and *mansoni* ♂♂ x *japonicum* ♀♀ were sufficient miracidia available for futher experiments (Vogel, 1942). Vogel exposed snail hosts of *S. japonicum* and *mansoni* to miracidia from both crosses. As hosts for *japonicum* he used specimens of *Oncomelania hupensis;* the hosts of *mansoni* were *Planorbis guadaloupensis* (*Australorbis glabratus*) and *P. pfeifferi* (*Biomphalaria pfeifferi*). The only infections obtained by him were with miracidia from the *mansoni* females in *P. pfeifferi,* a natural host for *mansoni.* Sixteen specimens of *P. pfeifferi* were infected, giving a percentage of infection of 9.5 based on the number of snails which survived and were examined. In mice and hamsters the cercariae from 13 of these snails developed into male worms and those from three into females. All the worms resulting from these cercariae were normal-appearing specimens of *S. mansoni.* In ♂-♀ infections the females produced eggs. Miracidia developed in the eggs and were infective for snails. The cercariae from these infections also developed in mice into typical male and female *S. mansoni.*

Vogel concluded that eggs of female *S. mansoni* in the crosses with male *japonicum* probably developed parthenogenetically, either spontaneously or as a result of stimulation by spermatozoa of male *japonicum.* Although he did not prove that parthenogenesis occurred, this conclusion seems to be justified, for the miracidia from these eggs infected only snail hosts of *S. mansoni,* and furthermore, all the progeny of these miracidia were typical of *mansoni* through two adult generations.

Vogel examined eggs in sectioned host tissues in an attempt to determine the chromosome number of developing miracidia in both his crosses between *japonicum* and *mansoni.* He also hoped to determine the behavior of the polar bodies and whether the spermatozoa played any part in development of the eggs. In these attempts he was unsuccessful because the large majority of eggs were dead or otherwise incapable of development. He did, however, find the diploid number of chromosomes (16) in sections of developing cercarial embryos of both sexes derived from *mansoni* females crossed with *japonicum* males. The normal chromosome number of *S. douthitti* has not been reported, and as yet no cytological studies have been made on my material. Therefore the chromosomal condition of the uniparental miracidia of *S. douthitti* and their progeny is not known.

As I have pointed out (unpublished), Vogel found that the eggs in his crosses between *S. japonicum* and *mansoni* were much less viable than eggs (presumably fertilized) from ♂-♀ infections with either species of fluke. In these crosses the large majority (90 to over 95%) of the eggs were dead (calcified or granular) with only a very small proportion containing normal embryos and miracidia, while in the usual ♂-♀ infections with either species of fluke Vogel found over half the eggs to be newly-laid or with embryos and miracidia.

In contrast to the results in Vogel's crosses I have found a much larger percentage of the eggs in unisexual infections with *S. douthitti* develop to miracidia; and from this comparison it was concluded that eggs of *douthitti*

have a greater ability to develop parthenogentically than do those of *S. japonicum* or *mansoni* (Short, unpublished).

While it is true that eggs of normal female *S. douthitti* (in unisexual infections) showed a much greater ability to develop parthenogenetically than eggs of *S. mansoni* and *japonicum* (in crosses), this was not true for eggs of female *S. douthitti* derived from uniparental miracidia. For in unisexual infections with such females the general picture regarding egg types corresponded closely to that described by Vogel in his crosses. In both cases the large majority of eggs were dead, and but very few embryos and miracidia were seen. In *S. douthitti*, then, the capacity for development of second generation parthenogenetic eggs was much reduced in comparison with unfertilized eggs of normal females; and the ability of these second generation parthenogenetic eggs to develop was comparable to that of the presumably unfertilized eggs of *S. mansoni* and *japonicum* in Vogel's crosses.

In my experiments several findings combine to indicate that the parthenogenetic miracidia of *S. douthitti* and their progeny were less viable than specimens derived from fertilized eggs. This impression is given by the low percentage of snail infections produced by uniparental miracidia, the abnormal behavior of some of the cercariae, and the low percentage of worms recovered from mice exposed to these cercariae. Correlated with this reduced viability is the observation that uniparental miracidia and the adult worms derived from them were smaller than normal specimens. The results of measurements of cercariae, while not conclusive, also suggest that those derived from uniparental miracidia tend to be smaller than normal. All these findings on miracidia, cercariae and adults indicate that the parthenogenetic stocks were less hardy than specimens derived from fertilized eggs. An explanation for this smaller size and apparent reduction in vitality of these parthenogenetic animals is not known. It may be a result of haploidy or of some other chromosomal abnormality caused by lack of fertilization. This, however, is only a conjecture, for cytological studies have not yet been made.

Vogel also found that miracidia which resulted from his crosses of *S. japonicum* ♂♂ x *mansoni* ♀♀ and of *mansoni* ♂♂ x *japonicum* ♀♀ were not as infective for snails as were normal miracidia. As indicated above, he obtained only negative results in exposures of snails to miracidia from *japonicum* females. The miracidia from *mansoni* females were capable of infecting snails, but a very low percentage of infection was realized, much lower than when normal miracidia were used. All the progeny of these miracidia, however, were apparently normal for *S. mansoni*.

An interesting result in my work is the finding that both male and female-producing cercariae developed from uniparental miracidia. It was noted that only one sex of cercariae emerged from each of the five snails infected with such miracidia. From this fact, together with the very low percentage of infected snails, we may assume that each snail was infected with only one miracidium. Vogel's results with miracidia from his cross between *S. japonicum* ♂♂ and *mansoni* ♀♀ were similar to mine in this respect; for he found infections with these miracidia gave rise to both male- and female-producing

cercariae, with only one sex of cercariae coming from each snail. Since it has been demonstrated that sex in schistosomes is already determined in the miracidium, the above results suggest that the females are heterogametic. However, one should not draw a definite conclusion regarding this matter, for the normal mechanism of sex determination in schistosomes is still uncertain. Ikeda and Makino (1936) and Niyamasena (1940) failed to demonstrate sex chromosomes in either males or females of *S. japonicum* and *mansoni*, and, as pointed out above, cytological studies on *S. douthitti* have not yet been reported.

Another interesting similarity between my results and Vogel's is the sex ratio of the cercariae derived from parthenogenetic miracidia. Vogel obtained a sex ratio of 13 males to 3 females in snail infections with miracidia from female *S. mansoni* crossed with male *japonicum*. In my work fewer snail infections were obtained, but the male to female ratio (4:1) was approximately the same.

In Vogel's experiments and in mine a higher percentage of male infections was realized than would be expected in infections of snails with single normal miracidia; for with normal miracidia a sex ratio of approximately 1:1 usually occurs. The reason for this preponderance of male infections is not known, but it may be that male- and female-determined eggs are produced in equal numbers and the parthenogenetic female stocks are less viable than the male. Evidence suggests that larval stages of females of *S. japonicum* (Faust, 1927) and *mansoni* (Pifano, 1948) in naturally infected snails are less resistant than those of males to adverse environmental conditions. It thus seems that the molluscan phases of normal females of these species may be less hardy than those of normal males. This may be true also for *S. douthitti*, and any further reduction in viability of parthenogenetic stocks, may be more evident in the female lines than in the male.

SUMMARY

Uniparental miracidia of *Schistosomatium douthitti* (i.e. miracidia which develop parthenogenetically in unisexual infections) appear entirely normal in structure and activity. However, measurements show that such miracidia are smaller than those derived from ♂-♀ infections (presumably from fertilized eggs).

Uniparental miracidia proved infective for snails, but less infective than miracidia from ♂-♀ infections. Of 373 young laboratory-reared snails (*Lymnaea palustris* and *stagnalis*) exposed to uniparental miracidia (some individually to single miracidia, others *en masse* to many miracidia), five snails were infected, giving a percentage of infection of 1.6, based on the 307 survivors.

Cercariae derived from uniparental miracidial infections were infective for mice. Cercariae from four snails gave rise to male worms only; those from one snail to females only. A lower percentage of recovery of worms was realized from cercariae derived from uniparental miracidia than from normal

cercariae; and the cercariae from three of the five snails infected with uniparental miracidia appeared to survive for a shorter free-living period than normal cercariae.

Adult worms derived from uniparental miracidia were reared only in unisexual infections. In these infections both male and female worms appeared normal except for size, which was smaller than that of normal specimens in unisexual infections of comparable ages.

Male and female worms derived from uniparental miracidia matured sexually in unisexual infections. The females laid eggs, most of which, when examined in fresh tissues, appeared to be dead and degenerate (infections 41-44 and 60-70 days old). However, miracidia developed in a small proportion of these eggs. Such miracidia evidently had developed parthenogenetically, for an examination of stained whole mounts of these females revealed no spermatozoa.

REFERENCES

CORT, W. W. 1915—Some North American larval trematodes. Illinois Biol. Monogr. 1(4): 447-532.

——— AND B. S. TALBOT 1936—Studies on schistosome dermatitis. III. Observations on the behavior of the dermatitis-producing schistosome cercariae. Am. J. Hyg. 23(2): 385-396.

FAUST, E. C. 1927—The possible presence of male schistosomes alone in experimental and natural infections. J. Parasitol. 14(1): 62-63.

IKEDA, K. AND S. MAKINO 1936—Studies on the sex and chromosomes of the oriental human blood fluke, *Schistosomum japonicum* Katsurada. J. Fac. Sc., Hokkaido Imp. Univ. s. 6, 5(1): 57-71.

NIYAMASENA, S. G. 1940—Chromosomen und Geschlecht bei *Bilharzia mansoni*. Ztschr. Parasitenk. 11(5): 690-701.

PENNER, L. R.—Morphological and biological studies on certain helminths of the muskrat. Unpublished thesis, Univ. Minnesota, Submitted 1940.

———1942—Studies on dermatitis-producing schistosomes in eastern Massachusetts, with emphasis on the status of *Schistosomatium pathlocopticum* Tanabe, 1923. J. Parasitol. 28(2): 103-116.

PIFANO, C. F. 1948—La infección uni-sexual producida por *Schistosoma mansoni* en condiciones experimentales. Arch. Venezolanos de Patol. Trop. y Parasit. Méd. 1(1): 63-72.

PRICE, H. F. 1931—Life history of *Schistosomatium douthitti* (Cort). Am. J. Hyg. 13(3): 685-727.

SHORT, R. B. 1948—Infective uniparental miracidia of *Schistosomatium douthitti* (Trematoda: Schistosomatidae). J. Parasitol. 34(6) Suppl.: 30.

VOGEL, H. 1941—Über den Einfluss des Geschlechtspartners auf Wachstum und Entwicklung bei Bilharzia mansoni und bei Kreuzpaarungen zwischen verschiedenen Bilharzia-Arten. Zentralbl. Bakteriol. I. Abt. Orig. 148: 78-96.

———1942—Über die Nachkommenschaft aus Kreuzpaarungen zwischen Bilharzia mansoni und B. japonica. Zentralbl. Bakteriol. I. Abt. Orig. 149: 319-333.

Two New Species of Oochoristica from Minnesota Skunks*

Asa C. Chandler

Rice Institute, Houston, Texas

In a collection of worms from Minnesota supplied to the writer by Dr. F. G. Wallace for use at the University of Minnesota Biological Station, there were included two vials containing worms of the genus *Oochoristica*, one lot from the spotted skunk, *Spilogale interruptus*, collected near Minneapolis, the other from *Mephitis* sp., presumably *M. m. hudsonica*, collected at Lake Itasca, Minnesota. Each of these two lots of worms was found to represent previously undescribed species, although a distinct species of *Oochoristica* has already been described from each of these genera of skunks in North America. *O. mephitis* Skinker, 1935 was described from *Mephitis elongata* in Georgia, and has subsequently been reported by Choquette (1951) in *M. mephitis* in Quebec. *O. oklahomensis* Peery, 1939 was described from *Spilogale interruptus* in Oklahoma.

Oochoristica wallacei n. sp.

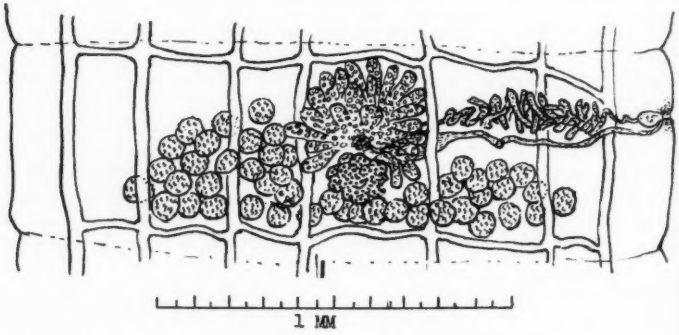
Figs. 1, 2

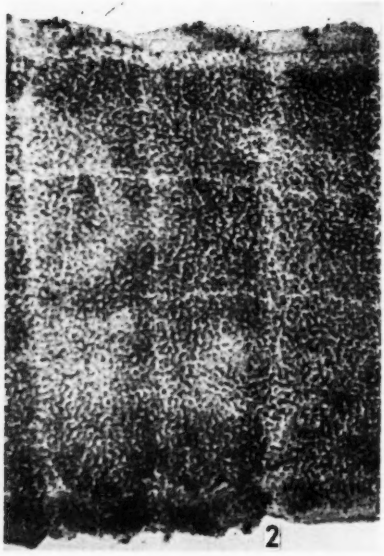
Description.—Strobila 80 to 95 mm. long, 0.75 to 1 mm. wide immediately behind scolex, gradually increasing to maximum width of 2.85 mm. at posterior end. Proglottids 165 to 250 in number. Scolex 775 to 900μ in diameter across region of suckers, bluntly rounded or truncated anteriorly, not demarcated from neck posteriorly. Posterior border of suckers only 300 to 375μ from anterior end. Suckers round, 200 to 225μ in diameter. Evidence of segmentation begins less than 1 mm. behind scolex. Margin of worm only slightly serrate, almost smooth in anterior third. Genital pores unilateral, about 30 to 35μ deep, and narrower than deep, situated between 1/4 and 1/3 length of segment from anterior border. Mature proglottids 350-500μ long and 2 to 2.4 mm. wide; ripe proglottids about 700-800μ long by 2.85 mm. wide. Longitudinal excretory canals 6 to 9 in number, dorsal ones not distinguishable from ventral. Cross connections near junction of segments, but not continuous from side to side. Genital ducts pass dorsal or ventral to two excretory vessels nearest poral side in an irregularly alternating manner, but seminal receptacle always dorsal to third excretory vessel.

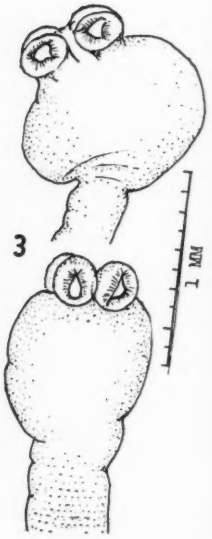
Testes 42 to 50 in number, anteroposteriorly elongated, in fully mature segments measuring 88-100 x 50-65μ, about 25 to 30 on aporal side of ovary, one row of about 4 posterior to ovary, the rest on poral side. Cirrus pouch

* Contribution from Biology Department, Rice Institute, and University of Minnesota Biological Station, Douglas Lodge.

75-88 x 60-63μ, opening into postero-medial portion of genital atrium, extending about half distance from bottom of genital pore to poral excretory canal. Vas deferens very tortuous, filled with sperm, occupying a considerable space in antero-poral portions of segment but not traceable beyond poral border of ovary. Deferent canal somewhat sinuous inside cirrus pouch.







Figs. 1-3.—1. Mature proglottid of *Oochoristica wallacei*, dorsal view; 2. Photomicrograph of ripe proglottid of *O. wallacei* showing very numerous small eggs, ×27.5; 3. Scoleces of *Oochoristica pedunculata*, showing inflation and pedunculated suckers.

Ovary somewhat nearer poral side of segment, made up of about 30 to 35 finger-like lobes, about 385 to 400μ broad and 300 to 350μ long. Vitelline gland posterior to central part of ovary, with 10 or 13 blunt lobes, about 185 to 217μ broad and 155 to 186μ long. Ootype in center of ovary-vitellarium complex. Vagina a nearly straight tube except for one or two kinks, passing inward from genital pore just posterior to vas deferens, bending posteriad near poral border of ovary, and enlarging into a spindle-shaped seminal receptacle 150 to 175μ long and about 75μ in diameter. Ripe proglottids entirely filled by uterus, which contains very large numbers of small eggs about 31 to 35μ in diameter, containing onchosphere about 26 to 27μ in diameter.

Host: *Spilogale interruptus* (Raf. 1820).

Locality: Minneapolis, Minnesota.

Type: U. S. Nat. Mus. Helm. Coll. No. 47815.

Of other species of *Oochoristica* in carnivores, only *O. herpestis* Kofend, 1917 approaches *wallacei* in width, but in *herpestis* the cirrus pouch extends to the lateral excretory vessels, the genital pores are irregularly alternating, there is no seminal receptacle, and the eggs are *much* larger. *O. wallacei* resembles the other three species of *Oochoristica* from North American skunks (*O. mephitis*, *O. oklahomensis* and *O. pedunculata*) in having unilateral genital pores, but it is a much broader worm than any of these. It is a much longer worm than *O. mephitis*, with about four times as many proglottids; other differences are the much larger scolex; the large cirrus pouch which, however, does not reach the poral excretory vessel as it does in *mephitis*; testes about twice as large in diameter; and irregular alternation of the genital ducts dorsal and ventral to the lateral excretory vessels. From *oklahomensis* it differs in being over twice as broad, in the larger scolex and smaller suckers, and in the smaller eggs. From *pedunculata*, aside from the striking difference in the scolex, it differs also in the character of the excretory vessels, the failure of the cirrus pouch to reach the lateral excretory vessel, and the much smaller eggs.

Oochoristica pedunculata n. sp.

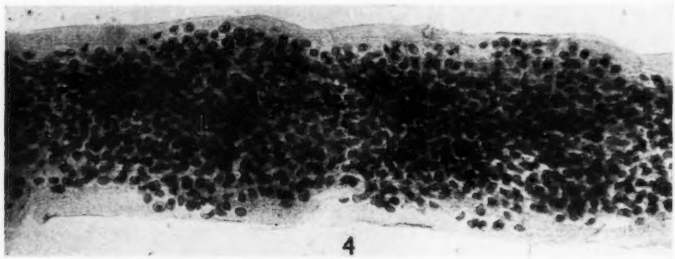
Figs. 3-5

Description.—Strobila estimated 80-125 mm. long ,with serrated margins about 295μ wide just behind scolex, gradually increasing to maximum width of 1 to 1.5 mm. Scolex expanded bulb-like in three of four specimens, about 900μ broad and 775μ long; in one specimen 465μ wide behind suckers, merging into neck. Suckers large, protruding on short stalks, and measuring from 250 x 250 to 320 x 217μ, with thin walls and large cavities. Neck begins abruptly in specimens with bulb-like scoleces. Evidence of segmentation begins about 600μ behind scolex, first segment about 95μ long. Mature segment from 950μ to 1.35 mm. wide and 350 to 600μ long, depending on state of contraction. Ripe segments from 1.5 mm. wide by 1 mm. long to 1.1 mm. wide by 1.5 mm. long. Genital pores unilateral, anterior to middle of length of segment. Genital atria about 40-42μ deep. Genital ducts pass

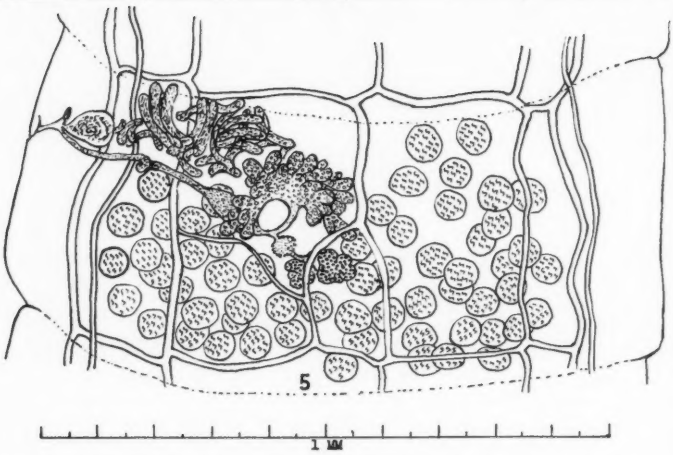
ventral to excretory ducts in most segments, but dorsal to them in some. A narrow dorsal excretory vessel and two broader ventral excretory vessels on each side, the latter connected by commissures near junction of segments, but dorsal vessel without commissures.

Testes about 40 to 65 in number, spherical, about 60-70μ in diameter, situated laterally and posteriorly to ovary and vitellaria, occasionally a few dorsal to these glands. Cirrus pouch about 70-85 x 42-60μ, reaching to, or almost to, lateral excretory vessel. Vas deferens extremely tortuous, forming a mass of convolutions increasing with age of segment, in anterior poral portion of segment, ending near middle of segment.

Ovary situated in middle or slightly porad of middle of segment, made up of about 25 blunt finger-like lobes, occupying space averaging about 175 by



4



5

1 MM

Figs. 4, 5.—4. Photomicrograph of ripe proglottids of *O. pedunculata,* showing relatively small numbers of large eggs, ×25.7. 5. Mature segments of *O. pedunculata,* dorsal view.

175μ. Vitellarium behind middle part of ovary, composed of about 6 to 10 blunt lobes, about half as wide and half as long as ovary. Vagina posterior to vas deferens, curving posteriad and forming seminal vesicle about 90 to 100μ long and 45μ in diameter, dorsal to poral side of ovary. Ootype and Mehlis gland between ovary and vitellarium, about 42μ in diameter. Oviduct joins vagina just median to seminal vesicle; fertilization canal continues posteromedially from there to ootype, which is joined from the aporal side by the vitelline duct. Ripe proglottids filled with eggs except along lateral margins. Eggs large, oval, from 55 to 65μ in length by 45 to 55μ in diameter, with embryos about 32 to 34μ in diameter, containing hooks 21μ long.

Host: *Mephitis* sp. (presumably *M. mephitis hudsonica*).

Locality: Lake Itasca, Minnesota.

Type: U. S. Nat. Mus. Helm. Coll. No. 47816.

O. pedunculata differs strikingly from all other species of the genus in the characters of the scolex, which in most specimens is expanded bulb-like (perhaps an artifact) and has pedunculate suckers. As in *O. wallacei* the genital ducts pass dorsal or ventral to the lateral excretory vessels in an irregularly alternating manner. The eggs are much larger than in any of the other species of *Oochoristica* from skunks; the onchospheres are as large as the entire eggs of *O. wallacei*. In the topography of the mature segments this species closely resembles *O. oklahomensis*.

REFERENCES

CHOQUETTE, L. P. E. 1951—Helminthes parasites trouvé chez la moufette *Mephitis mephitis* dans la Province de Quebec. Canad. J. Comp. Med. and Vet. Sci. 15: 62-64.

KOFEND, L. 1917—Cestoden aus Säugetiere und aus *Agama colonorum*. Ans. Akad. Wissensch. Wien, Math-Naturw. Kl. 54: 229-231.

PEERY, H. J. 1939—A new unarmed tapeworm from the spotted skunk. J. Parasit. 25: 487-490.

SKINNER, M. S. 1935—A new species of Oochoristica from a skunk. J. Wash. Acad. Sci. 25: 59-65.

Host Relationships and Seasonal Abundance of Some Southwest Georgia Ectoparasites[1]

Harvey B. Morlan

Federal Security Agency, Plague Field Study,
St. Michael's College, Santa Fe, New Mexico

The increasing knowledge of animal ectoparasites as factors in the transmission of disease serves to emphasize the need for additional taxonomic and ecologic information. The transmission of epidemic typhus fever by lice, of Rocky Mountain spotted fever by ticks, and of plague by fleas are well-known examples of ectoparasitic involvement in human disease. The economic and medical importance of the various groups of ectoparasites have been treated in such texts as Herms (1939), Mackie, Hunter, and Worth (1945), Hull (1947), and Matheson (1950). One instance of a recent contribution to our knowledge of the relation of ectoparasites to disease is given in a report by Huebner, Jellison, and Pomerantz (1946), who showed the mouse mite, *Allodermanyssus sanguineus* Hirst, to be a vector of rickettsialpox.

An unusual opportunity to secure extensive records of host-ectoparasite relationships was afforded the author during an investigation of murine typhus fever in southwestern Georgia. An initial over-all account of the typhus study has been given by Hill and Morlan (1948).[2] From October 1945 through April 1949, a total of more than 506,000 arthropods were collected from 32,320 mammals. Domestic rats accounted for 28,571 of the mammals examined. The remainder were representative of 29 other species collected in connection with the serological survey for murine typhus infection reported by Morlan, Hill, and Schubert (1950). Interest in the interchange of ectoparasites among different species of mammals was heightened by the serologic findings. Forty-seven sera from 12 species of animals (exclusive of domestic rats) were positive to the complement fixation test for murine typhus.

Complete collection records are summarized in the present report without any attempt at special note of new host or locality associations. Several new species have been described from specimens collected and others are presently in the possession of specialists. Reliable information on seasonal variation in ectoparasite abundance was possible only in a relatively few species where sufficient data were obtained.

---

1 From Communicable Disease Center, Public Health Service, Federal Security Agency, Atlanta, Ga. Based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Texas Technological College, Lubbock, Texas, May 1950.

2 The study was made in cooperation with the Georgia Department of Public Health, C. D. Bowdoin, Director, Division of Preventable Diseases, and Roy J. Boston, Director, Typhus Control Service.

ACKNOWLEDGMENTS

The author is grateful to the many individuals who have contributed to the study. Thanks are due to E. W. Stafford of Mississippi State college and H. D. Pratt of the U. S. Public Health Service for determinations of Mallophaga and Anoplura; to W. S. Fisher of the U. S. Department of Agriculture and E. A. Chapin of the U. S. National Museum for Coleoptera; to Alan Stone and C. W. Sabrosky of the U. S. Department of Agriculture for Diptera; to C. F. W. Muesebeck of the U. S. Department of Agriculture and M. A. Stewart of the University of California for Siphonaptera; and to E. W. Baker, F. C. Bishopp, and C. N. Smith of the U. S. Department of Agriculture, R. W. Strandtmann of the Texas Technological College, G. H. Wharton of Duke University, R. W. Keegan of the U. S. Army, and C. D. Radford of the British Museum for determinations of Acarina.

In the trapping and determination of mammals, the generous assistance and advice of E. V. Komarek, Thomasville mammalogist, is gratefully acknowledged.

For advice and counsel at various times during the conduct of the Typhus Investigations Project, the writer is indebted to many Public Health Service officials, especially to G. H. Bradley, J. J. Essex, E. L. Hill, A. G. Gilliam, V. B. Link, G. E. Quinby, S. E. Miller, and A. D. Langmuir.

The author is grateful to the many project members whose conscientious work made possible the large collections. Special mention is due J. E. Dent for highly effective supervision of trapping activities and Mrs. M. V. Griffin for efficient assistance in the tedious sorting and recording of ectoparasites.

Methods.—From October 1945 to January 1949, monthly samples of the domestic rat population were taken from Decatur, Thomas, and Brooks counties in Georgia. Trapping was begun during April 1946 in Grady County and continued with trapping in Thomas and Brooks counties through April 1949. Field activities in Decatur County were terminated at the end of January 1949. Comparatively small numbers of rats were secured between August 1946 and April 1947 from Cook County in connection with a supplementary ectoparasite control experiment previously described by Morlan (1948).

Most of the mammals other than domestic rats were collected from Decatur, Grady, Thomas, and Brooks counties during 1947 and 1948. Wildlife collections were predominately from the fields and woods. However, the opossum, cotton rat, wood rat, and spotted skunk were occasionally trapped in number 0 steel traps that were set in buildings for collection of domestic rats. Native rats and mice were caught alive in several types of traps. Opossums and carnivorous mammals were caught in number 0 to number 2 steel traps. Many of the squirrels and rabbits were taken with a shotgun.

Only animals that were taken alive or immediately after death were used in the survey. Such animals were placed in fine-mesh cloth bags, tagged with collection data, and brought to the Thomasville laboratory. Each animal was given a number which was used for subsequent identification of ectoparasites, and for blood samples. After a blood specimen was taken, an animal was returned to its cloth bag and kept for a minimum period of 15 minutes in a chloroform jar. Over a white enameled pan, the animal was brushed vigorously with a stiff-bristled typewriter-key brush. In

addition to the thorough brushing, the animal was examined for sticktight fleas or other ectoparasites that require removal with forceps. Chiggers, found in the ears or in brushings of the animals, were collected. Such collections are not considered complete since there was no special effort to carefully search the entire body of each host for these larval mites. The cloth bags were turned inside-out to recover any parasites that had dropped off. To assure thorough collection, periodic checks were made to see whether any ectoparasites remained on previously brushed animals. The number of common ectoparasites missed was too small to influence figures of average abundance.

Mites and lice were removed from the pans with sharpened applicator sticks and placed in streaks of glycerin on microscope slides for preliminary determination and counting under a dissecting microscope. Fleas were collected in 22 mm Syracuse dishes containing 10 percent potassium hydroxide for clearing preliminary to determination. All specimens of unknown or doubtful identity, as well as occasional samples of the more commonly collected ectoparasites were sent to specialists for determination.

Ectoparasite-host relationships.—Table 1 provides a compact host-ectoparasite index. It lists both common and scientific names of the species of mammals collected. The classification is according to Simpson (1945). Numbers, following the name of each species of mammal, refer to Table 2 where mammals are listed by common name under each numbered species of arthropod.

Forty-nine species of arthropods were collected from 20,489 roof rats;[3] 41 from 8,082 brown rats; 30 from 966 cotton rats; 27 from 349 opossums; 17 each from 215 cottontails, 101 gray squirrels, 110 Florida skunks, 102 spotted skunks; 16 from 249 cotton mice; 15 each from 243 old-field mice, 520 house mice, 100 raccoons; 12 from 14 foxes; and 11 each from 377 little brown bats, 42 fox squirrels, 220 domestic cats. Other species of mammals were represented in the collection by 38 or less specimens; 10 or less species of arthropods were collected from each.

Table 2 gives easy reference to the host relationships and abundance of ectoparasites. The animals are listed by common name in phylogenetic order under each species of arthropod. Data for each species of mammal include number examined, number infested with one or more specimens of the parasitic species, and number of parasites collected.

Species of insects are listed alphabetically under each family. The genera of the order Mallophaga were referred to families as suggested by Dr. E. W. Stafford of Mississippi State College. The classification of Hubbard (1947) has been used for the Siphonaptera. This agrees with Ewing and Fox (1943) except that the latter authors place the genus *Conorhinopsylla* in the Dolichopsyllidae rather than in the Hystrichopsyllidae.

---

3 Abbreviated or common names for species are frequently used throughout the text and tables to conserve space. Complete names are shown for mammals in Table 1, for arthropods in Table 2.

In general, the Acarina follow the arrangement of Vitzthum (1941). Slight modifications and the placement of new species are in accordance with suggestions from Dr. R. W. Strandtmann of Texas Technological College.

Occasional or accidental ectoparasites are recorded in Table 2 without further comment. Arthropods not known to be ectoparasites have been designated with an asterisk in the tabulation. In many species of ectoparasites the principal host is apparent from the data given. However, it is probable that the common host of some species was not represented in the collections. For example, the sticktight flea, *Echidnophaga gallinacea* (Westwood), is a common pest of domestic fowls which are not included in the host lists.

Between April 1946 and September 1947 most of the domestic rat runs and harborages in Thomas and Brooks counties were dusted five times with 10 percent DDT. A considerable reduction of ectoparasites, especially fleas, was obtained. Larger numbers of *Rattus rattus* were taken from dusted than from untreated areas. Data from all areas are combined in the present report so that comparison of relative ectoparasite abundance on the two species of domestic rats does not necessarily reflect normal proportions. For example, *E. gallinacea* was found as a parasite on about 20 per cent of *Rattus norvegicus*, while only slightly more than 2 percent of *R. rattus* were infected. *R. norvegicus* is normally more heavily parasitized with this flea than is *R. rattus*, but the figures given have also been influenced by the proportionately larger collections of *R. rattus* than *R. norvegicus* from DDT dusted areas. Dusting probably had no significant effect on ectoparasites of the other animals which did not have close contact with DDT dust.

Although *Laelaps nuttalli* Hirst (=Laelaps hawaiiensis Ewing) and *Hoplopleura oenomydis* Ferris have been recorded from domestic rats in many southern states, they have not been encountered in the southwestern Georgia collections.

While over 506,000 arthropods were collected, only about 460,000 are listed in Table 2. Specimens that were lost, damaged, or identified only to a group larger than genus were excluded from the table. Most of the excluded specimens were Listrophoridae, 7,116 mites of this family were collected from a single bobcat and about 30,000 from a single cottontail.

Noteworthy records of the maximum number of ectoparasites collected from a single host animal include: *Felicola subrostrata* (Nitzch)—64 on domestic cat; *Neotrichodectes mephitidis* (Osborn)—220 on Florida skunk; *Neotrichodectes osborni* Keler—30 on spotted skunk; *Suricatoecus octomaculatus* (Paine)—42 on raccoon; *Hoplopleura hesperomydis* (Osborn)—21 on cotton mouse; *Hoplopleura hirsuta* Ferris—843 on cotton rat; *Neohaematopinus sciurinus* (Mjöberg)—42 on gray squirrel, 23 on fox squirrel; *Polyplax spinulosa* (Burmeister)—3452 on brown rat, 2572 on roof rat; *E. gallinacea*—929 on brown rat, 130 on roof rat, 130 on opossum; *Cediopsylla simplex* (Baker)—30 on cottontail; *Ctenocephalides felis* (Bouché)—158 on domestic cat, 135 on opossum; *Xenopsylla cheopis* (Rothschild)—219 on

roof rat, 181 on brown rat, 8 on house mouse; *Orchopeas howardi* (Baker)—102 on fox squirrel; *Polygenis gwyni* (C. Fox)—58 on opossum, 25 on cotton rat; *Ctenophthalmus pseudagyrtes* Baker—18 on pine mouse; *Leptopsylla segnis* (Schönherr)—126 on brown rat, 73 on roof rat, 17 on cotton rat, 16 on house mouse; *Haemolaelaps geomys* Strandtmann—148 from pocket gopher; *Haemolaelaps glasgowi* (Ewing)—206 on cotton rat, 40 on opossum; *Haemolaelaps megaventralis* (Strandtmann)—76 on gray squirrel, 68 on fox squirrel; *Echinolaelaps echidninus* (Berlese)—96 on brown rat; *Bdelonyssus bacoti* (Hirst)—2119 on roof rat, 957 on brown rat, 182 on rice rat, 123 on domestic cat, 67 on opossum, 65 on cotton mouse, 52 on cotton rat, 29 on house mouse; *Neoichoronyssus wernecki* (Fonseca)—44 on cotton rat, 42 on opossum; *Hirstionyssus staffordi* Strandtmann & Hunt—43 on spotted skunk; *Listrophorus bakeri* Radford—696 on cotton rat.

Records of interchange of ectoparasites among host species indicate possible vectors of disease (Table 3). The commonly encountered domestic rat ectoparasites, *P. spinulosa, X. cheopis, L. segnis,* and *B. bacoti,* are found as occasional parasites on a variety of other mammals. Domestic rats are occasional hosts to many species of ectoparasites which are more commonly found on other mammals.

Table 3 lists only the host species represented in the southwestern Georgia collection by 14 or more specimens. Of those listed, blood sera positive to the murine typhus complement fixation test were obtained from the opossum, cottontail, fox squirrel, rice rat, cotton mouse, old-field mouse, cotton rat, brown rat, roof rat, house mouse, and Florida skunk. The mites, *H. glasgowi* and *B. bacoti,* have been found on all of these mammals except the fox squirrel; *C. felis* was lacking only from the rice rat and old-field mouse; *X. cheopis* was not found on the cottontail, fox squirrel, rice rat, or Florida skunk.

Seasonal abundance.—Reliable data on seasonal abundance of ectoparasites have been obtained for only a few species. Many arthropods were collected in insufficient numbers or were taken from host animals that were not obtained at regular intervals throughout the year. Seasonal abundance of the most common domestic rat ectoparasites, *X. cheopis, L. segnis, B. bacoti,* and *P. spinulosa,* has been reported by Hill and Morlan (1948) for the period from October 1945 through April 1948. It is anticipated that further data on these species will be given in a future report on residual effectiveness of DDT dust in murine typhus control.

Seasonal abundance of several species of ectoparasites is based on records from the cotton rat. Small numbers of cotton rats collected prior to January 1947 and after April 1948 were not considered in the monthly tabulations. Nine or more cotton rats were collected each month from January 1947 to May 1948.

Of 966 cotton rats, over 75 percent were infested with one or more specimens of *H. hirsuta.* A regular seasonal trend in abundance of this louse was not apparent. Infestation of cotton rats varied from 93 percent of 47 rats examined in February 1947 to 25 percent of 12 rats examined in

August 1947. The average number of lice per rat varied from more than 65 in September 1947 to only 1 in August 1947.

In untreated Grady County, *E. gallinacea* was found on more than 7 percent of the roof rats collected in June 1946, 15 percent in the same month of 1947, and more than 9 percent in July 1948. The highest average number of fleas per rat was about 1 in November 1947. Low percentages of infestation occurred in February 1947, January 1948, and March 1949.

Brown rats from Grady County were more heavily infested with *E. gallinacea* in July 1946 (43 percent), April 1947 (34 percent), and July 1948 (more than 73 percent). The highest average number of fleas per rat was 17.2 in March 1947. Low rates of infestation were observed in February 1947, with nearly 7 percent, and February 1948, with less than 6 percent.

C. simplex occurred on nearly 39 percent of the 215 cottontail rabbits. This flea shows a very definite peak of abundance during winter months reaching up to 71 percent infestation in January 1947. Small monthly collections of cottontails were not found to be infested with *C. simplex* in August, September, and October during either 1947 or 1948. The highest average number of fleas per rabbit was 3.3 from 10 rabbits collected in February 1947.

P. gwyni was found on 50 percent of all cotton rats. The highest infestation rate was 85 percent in April 1948. More than 70 percent of the rats were infested with this flea in April and May of 1947 and March, April, July and August of 1948. The lowest infestation was 21 percent in January 1948. The average number of fleas per rat ranged from 6.4 in May 1947 to 0.4 in January 1948.

H. glasgowi was found on more than 74 percent of the 966 cotton rats. There does not seem to be any regular seasonal change in abundance of this mite. Infestation varied from a high of 96 percent of 28 rats in April 1948 to a low of 44 percent of nine rats in September 1947. The high and low in average number of mites per rat occurred in these same months and was 20.6 and 2.6 respectively.

H. megaventralis has been collected in small numbers during every month of the year but data were insufficient to indicate fluctuation in seasonal abundance.

E. echidninus was rarely found except on the brown rat and had a restricted local distribution. Of the 1,788 mites collected, 1,594 were found on brown rats from Thomas County. Further, most of the brown rats infested with this mite were taken only in the northwest corner of Thomas County. Only 1 specimen of this mite was obtained from more than 3,000 Decatur County brown rats.

In Thomas County the highest average number of *E. echidninus* per brown rat was 4.8 in May 1946, when nearly 23 percent of the 31 rats were infested. In April 1949 this same infestation rate was obtained with nearly 23 percent of 140 brown rats being infested with an average of more than

3 mites per rat. Infestation was present during all months and there did not appear to be any definite seasonal peak of abundance.

N. wernecki was more abundant on the opossum during the first six months of the year. It was not found during the months of July, August, or September, and was of rare occurrence in the last three months of the year.

Dermacentor variabilis Say was found on a wide variety of mammals during every month of the year. A few larvae were taken from raccoons during January, August, and October; nymphs during February, March, April, August, and October. Adults were more prevalent on raccoons collected during April, May, June, July, and August and absent during November, December, and January. *D. viriabilis* was not found on 25 cotton rats collected in June; only nymphs were found during March, April, and May; larvae and nymphs were collected during all remaining months of the year.

Haemaphysalis leporis-palustris (Packard) was prevalent on cottontail rabbits during all the monthly collections for a period of more than two years. All stages were obtained in every month with the exception that larvae were not found on 16 cottontails collected in May or nymphs on 5 cottontails examined during September. Infestation was heavier during the cooler months of December through April.

Summary.—More than 506,000 arthropods were collected from 32,320 mammals taken in southwestern Georgia from October 1945 through April 1949. Seven species of Mallophaga, 7 species of Anoplura, 1 of Hemiptera, 3 of Coleoptera, 5 of Diptera, 16 of Siphonaptera, and 66 species of Acarina were found on the 31 species of mammals represented in the collections. Actual or potential methods for spread of disease are apparent in the tabulation of host relationships and abundance of ectoparasites. Reliable information on seasonal variation in ectoparasite abundance was possible in a relatively few species where sufficient data were obtained.

REFERENCES

EWING, H. E. AND IRVING FOX 1943—The fleas of North America. U. S. Dept. of Agriculture, Misc. Pub. No. 500: 1-142.

HERMS, WILLIAM B. 1939—Medical entomology. Macmillan Co., New York: 1-582.

HILL, E. L. AND H. B. MORLAN 1948—Evaluation of county-wide DDT dusting operations in murine typhus control. Pub. Health Rep. 63: 1635-1653.

HUBBARD, C. ANDRESON 1947—Fleas of western North America. Iowa State College Press, Ames, Iowa: 1-533.

HUEBNER, ROBERT J., WILLIAM L. JELLISON AND CHARLES POMERANTZ 1946—Rickettsialpox—A newly recognized rickettsial disease—IV. Isolation of a rickettsia apparently identical with the causative agent of rickettsialpox from *Allodermanyssus sanguineus*, a rodent mite. Pub. Health Rep. 61: 1677-1682.

HULL, THOMAS G. 1947—Diseases transmitted from animals to man. Charles C. Thomas, Springfield: 1-571.

MACKIE, THOMAS T., GEORGE W. HUNTER AND C. BROOKE WORTH 1945—A manual of tropical medicine. W. B. Saunders, Philadelphia: 1-727.

MATHESON, ROBERT 1950—Medical entomology. Comstock Publishing Co., Ithaca, N. Y.: 1-612.

MORLAN, H. B. 1948—Dusts containing combinations of DDT, sulphur, and hydroxy pentamethyl flavan to control rat ectoparasites. J. Econ. Ent. 40: 917.

———, E. L. HILL AND J. H. SCHUBERT 1950—Serological survey for murine typhus infection in southwest Georgia animals. Pub. Health Rep. 65: 57-63.

SIMPSON, GEORGE GAYLORD 1945—The principles of classification and a classification of mammals. Bull. Am. Mus. Nat.. Hist. 85: 1-350.

VITZTHUM, H. GRAF 1941—Das System der Acari. In H. G. Bronn's Klassen und Ordnungen des Tierreichs, B. 5, IV Abt. 5 Buch. Acarina. Lieferung 5: 751-800.

TABLE 1.—A list of Southwest Georgia mammals examined with reference to arthropods collected during the period of October 1945-April 1949 (numbers refer to Table 2 where hosts are shown under each numbered species of arthropod).

Class Mammalia
Order Marsupialia
Family Didelphidae

Florida opossum, *Didelphis virginiana pigra* Bangs—10, 14, 24-28, 30, 31, 33, 36, 43, 51, 55, 56, 59, 60, 63, 66, 75, 76, 79, 82, 83, 86, 97, 99

Order Insectivora
Family Soricidae

Little short-tailed shrew, *Cryptotis parva* (Say)—(1 examined, not infested)
Family Talpidae

Howell mole, *Scalopus aquaticus howelli* Jackson—35, 50, 51, 65

Order Chiroptera
Family Vespertilionidae

Little brown bat, *Myotis lucifugus lucifugus* (LeConte)—14, 15, 19, 26, 28, 36, 64, 65, 67, 69, 70, 72

Seminole red bat, *Lasiurus borealis seminola* (Rhoads)—(4 examined, not infested)

LeConte lump-nosed bat, *Plecotus macrotis* (LeConte)—(1 examined, not infested)
Family Molossidae

LeConte free-tailed bat, *Tadarida cynocephala* (LeConte)—39, 55, 64, 65, 68

Order Lagomorpha
Family Leporidae

Eastern cottontail, *Sylvilagus floridanus mallurus* (Thomas)—21, 24-26, 30, 33, 36, 55, 63, 79, 82, 83, 90, 97-99, 105

Marsh rabbit, *Sylvilagus palustris palustris* (Bachman)—25, 26, 28, 30, 55, 62, 82, 83

Order Rodentia
Family Sciuridae

Southern gray squirrel, *Sciurus carolinensis carolinensis* Gmelin—10, 11, 13, 14, 24, 28, 31, 40, 55, 56, 63, 79, 82, 96, 97, 99, 100

Southern fox squirrel, *Sciurus niger niger* Linnaeus—10, 11, 26, 31, 36, 56, 59, 79, 82, 100, 104

Southeastern flying squirrel, *Glaucomys volans saturatus* Howell—12, 31, 34, 36, 56
Family Geomyidae

Georgia pocket gopher, *Geomys tuza tuza* (Barton)—54
Family Cricetidae

Swamp rice rat, *Oryzomys palustris palustris* (Harlan)—14, 33, 53, 55, 61, 63, 65, 82, 99, 101

Eastern harvest mouse, *Reithrodontomys humulis humulis* (Audubon & Bachman)—86

Cotton mouse, *Peromyscus gossypinus gossypinus* (LeConte)—8, 9, 14, 20, 26, 28, 32, 33, 35, 36, 51, 55, 59, 63, 82, 102

Old-field mouse, *Peromyscus polionotus polionotus* (Wagner)—8, 9, 14, 24, 28, 33, 35, 43, 55, 56, 59, 63, 82, 86, 95

Southern golden mouse, *Peromyscus nuttalli aureolus* (Audubon & Bachman)—63, 82
Eastern cotton rat, *Sigmodon hispidus komareki* (Say & Ord)—9, 14, 24, 26, 28, 30, 31, 33, 35-37, 40, 42, 43, 51, 55, 56, 59, 61, 63-66, 74, 80, 82, 83, 88, 97, 99, 102
Florida wood rat, *Neotoma floridana floridana* (Ord)—9, 14, 35, 55, 63, 82, 86
Pine mouse, *Pitymys pinetorum pinetorum* (LeConte)—14, 31, 35, 51, 55
Family Muridae
Brown rat, *Rattus norvegicus* (Erxleben)—14, 17, 18, 20, 22-24, 26, 28, 29, 31, 33, 35, 36, 41-47, 49, 52, 55-60, 63, 69, 73, 79, 80, 82, 83, 86-88, 94, 97
Roof rat, *Rattus rattus* (Linnaeus)—1, 14, 16, 20, 23-29, 31, 33, 35, 36, 38, 41-44, 46-48, 55-60, 63, 73, 75, 79, 82-89, 91-94, 97, 103, 105
House mouse, *Mus musculus* Linnaeus—14, 24-26, 28, 35, 36, 42, 43, 55, 56, 59, 63, 82, 83, 86
Order Carnivora
Family Canidae
Florida gray fox, *Urocyon cinereoargenteus floridanus* Rhoads—7, 24-26, 75, 76, 79-83, 97
Family Procyonidae
Florida raccoon, *Procyon lotor elucus* Bangs—6, 14, 25, 26, 28, 31, 33, 55, 63, 75-79, 82
Family Mustelidae
Southern weasel, *Mustela noveboracensis notia* (Bangs)—5, 75, 76
Florida skunk, *Mephitis elongata* (Bangs)—3, 11, 24, 26, 27, 33, 55, 59, 63, 65, 71, 75-77, 79, 82, 83
Spotted skunk, *Spilogale putorius* (Linnaeus)—4, 24, 26-28, 31, 33, 54-56, 59, 63, 71, 74, 75, 79, 82
Family Felidae
Florida bobcat, *Felis rufus floridanus* (Rafinesque)—24-26, 76, 79, 82
Domestic cat, *Felis domestica* Linnaeus—2, 24-26, 28, 33, 36, 63, 79, 82, 83

TABLE 2.—A list of arthropods collected in Southwest Georgia during the period of October 1945-April 1949. Abundance and host relationships are indicated under each species. Arthropods collected from the host pelage but not known to be ectoparasites are marked with an asterisk (*).

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
Class Insecta			
Order Mallophaga			
Family Philopteridae			
1. *Goniocotes hologaster* (Nitzch)			
Roof rat	20,489	1	2
Family Trichodectidae			
2. *Felicola subrostrata* (Nitzch)			
Domestic cat	220	7	139
3. *Neotrichodectes mephitidis* (Osborn)			
Florida skunk	110	5	444
4. *Neotrichodectes osborni* Keler			
Spotted skunk	102	4	69
5. *Neotrichodectes* sp.			
Weasel	3	1	10
6. *Suricatoecus octomaculatus* (Paine)			
Raccoon	100	32	467
7. *Suricatoecus vulpis* (Denny)			
Gray fox	14	2	28

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
Order Anoplura			
Family Haematopinidae			
8. *Hoplopleura hesperomydis* (Osborn)			
Cotton mouse	249	13	107
Old-field mouse	243	1	11
9. *Hoplopleura hirsuta* Ferris			
Rice rat	29	1	1
Cotton mouse	249	1	1
Old-field mouse	243	1	1
Cotton rat	966	720	10,532
Wood rat	38	1	5
10. *Hoplopleura sciuricola* Ferris			
Opossum	349	1	2
Gray squirrel	101	3	13
Fox squirrel	42	3	6
11. *Neohaematopinus sciurinus* (Mjöberg)			
Gray squirrel	101	15	87
Fox squirrel	42	17	457
Florida skunk	110	1	20
12. *Neohaematopinus sciuroptera* (Osborn)			
Flying squirrel	14	1	1
13. *Neohaematopinus* sp.			
Gray squirrel	101	4	14
14. *Polyplax spinulosa* (Burmeister)			
Opossum	349	5	7
Little brown bat	377	4	12
Gray squirrel	101	2	4
Rice rat	29	2	2
Cotton mouse	249	15	21
Old-field mouse	243	9	11
Cotton rat	966	13	15
Wood rat	38	4	4
Pine mouse	5	2	2
Brown rat	8,082	5,440	76,913
Roof rat	20,489	13,613	132,220
House mouse	520	35	50
Raccoon	100	2	3
Order Hemiptera			
Family Cimicidae			
15. *Cimex pilosellus* (Horv.)			
Little brown bat	377	many	many
Order Coleoptera			
Family Nitidulidae			
*16. *Carpophilus* sp.			
Roof rat	20,489	1	1
Family Cucujidae			
*17. *Laemophloeus minutus* (Oliv.)			
Brown rat	8,082	1	1
Family Colydiidae			
*18. *Aglenus brunneus* (Gyll.)			

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
Brown rat	8,082	1	1
Order Diptera			
Family Nycteribiidae			
19. *Basilia boardmani* Rozeboon			
Little brown bat	377	4	34
Family Cuterebridae			
*20. *Atrypoderma* sp.			
Cotton mouse	249	1	1
Brown rat	8,082	3	4
Roof rat	20,489	7	7
*21. *Cuterebra buccata* (F.)			
Cottontail	215	1	1
*22. *Cuterebra* sp.			
Brown rat	8,082	1	1
*23. *Pseudobogeria* sp.			
Brown rat	8,082	2	2
Roof rat	20,489	2	2
Order Siphonaptera			
Family Hectopsyllidae			
24. *Echidnophaga gallinacea* (Westwood)			
Opossum	349	33	322
Cottontail	215	5	10
Gray squirrel	101	2	4
Old-field mouse	243	1	1
Cotton rat	966	2	2
Brown rat	8,082	1,620	18,324
Roof rat	20,489	574	2,675
House mouse	520	3	17
Gray fox	14	1	2
Florida skunk	110	3	3
Spotted skunk	102	12	51
Bobcat	3	1	3
Domestic cat	220	53	466
Family Pulicidae			
25. *Cediopsylla simplex* (Baker)			
Opossum	349	9	12
Cottontail	215	83	276
Marsh rabbit	22	11	61
Roof rat	20,489	4	7
House mouse	520	1	10
Gray fox	14	8	34
Raccoon	100	2	2
Bobcat	3	1	18
Domestic cat	220	2	2
26. *Ctenocephalides felis* (Bouchè)			
Opossum	349	133	615
Little brown bat	377	1	1
Cottontail	215	14	18
Marsh rabbit	22	1	1
Fox squirrel	42	1	6
Cotton mouse	249	2	2

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
Cotton rat	966	4	5
Brown rat	8,082	238	413
Roof rat	20,489	80	102
House mouse	520	1	1
Gray fox	14	5	9
Raccoon	100	3	4
Florida skunk	110	9	21
Spotted skunk	102	10	18
Bobcat	3	1	2
Domestic cat	220	220	6,210
27. *Pulex irritans* Linnaeus			
Opossum	349	1	2
Roof rat	20,489	1	2
Florida skunk	110	3	11
Spotted skunk	102	2	3
28. *Xenopsylla cheopis* (Rothschild)			
Opossum	349	16	27
Little brown bat	377	1	1
Marsh rabbit	22	1	1
Gray squirrel	101	1	1
Cotton mouse	249	3	3
Old-field mouse	243	2	2
Cotton rat	966	18	30
Brown rat	8,082	3,056	22,797
Roof rat	20,489	4,129	22,428
House mouse	520	15	27
Raccoon	100	2	2
Spotted skunk	102	2	2
Domestic cat	220	3	3
Family Dolichopsyllidae			
29. *Nosopsyllus fasciatus* (Bosc)			
Brown rat	8,082	2	3
Roof rat	20,489	2	2
30. *Odontopsyllus multispinosus* Baker			
Opossum	349	3	3
Cottontail	215	30	81
Marsh rabbit	22	7	14
Cotton rat	966	1	1
31. *Orchopeas howardi* (Baker)			
Opossum	349	31	80
Gray squirrel	101	51	185
Fox squirrel	42	27	272
Flying squirrel	14	7	34
Cotton rat	966	1	1
Pine mouse	5	1	4
Brown rat	8,082	4	4
Roof rat	20,489	3	4
Raccoon	100	18	53
Spotted skunk	102	2	3
32. *Orchopeas leucopus* (Baker)			
Cotton mouse	249	1	1

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
33. *Polygenis gwyni* (C. Fox)			
Opossum	349	114	501
Cottontail	215	1	1
Rice rat	29	4	7
Cotton mouse	249	2	2
Old-field mouse	243	5	5
Cotton rat	966	483	1,899
Brown rat	8,082	19	23
Roof rat	20,489	21	23
Raccoon	100	6	7
Florida skunk	110	7	7
Spotted skunk	102	2	6
Domestic cat	220	1	2
Family Hystrichopsyllidae			
34. *Conorhinopsylla stanfordi* Stewart			
Flying squirrel	14	1	1
35. *Ctenophthalmus pseudagyrtes* Baker			
Howell mole	7	3	10
Cotton mouse	249	2	2
Old-field mouse	243	2	2
Cotton rat	966	8	9
Wood rat	38	1	1
Pine mouse	5	4	31
Brown rat	8,082	2	2
Roof rat	20,489	3	3
House mouse	520	1	1
36. *Leptopsylla segnis* (Schönherr)			
Opossum	349	3	3
Little brown bat	377	1	1
Cottontail	215	2	2
Fox squirrel	42	1	1
Flying squirrel	14	1	1
Cotton mouse	249	9	14
Cotton rat	966	26	54
Brown rat	8,082	1,680	10,648
Roof rat	20,489	3,901	19,254
House mouse	520	70	214
Domestic cat	220	3	9
37. *Stenoponia americana* (Baker)			
Cotton rat	966	2	2
38. *Peromyscopsylla scotti* I. Fox			
Roof rat	20,489	1	1
Family Ischnopsyllidae			
39. *Sternopsylla texana* (C. Fox)			
Free-tailed bat	6	1	1
Class Arachnida			
Order Acarina			
Family Parasitidae			
*40. *Parasitus americanus* Berlese			
Gray squirrel	101	1	1
Cotton rat	966	1	3

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
*41. *Blattiosocius tridons* Keegan			
Brown rat	8,082	1	1
Roof rat	20,489	4	5
Family Macrochelidae			
*42. *Macrocheles* sp.			
Cotton rat	966	1	1
Brown rat	8,082	5	5
Roof rat	20,489	6	56
House mouse	520	1	1
Family Laelaptidae			
*43. *Hypoaspis murinus* Strandtmann & Menzies			
Opossum	349	2	4
Old-field mouse	243	2	6
Cotton rat	966	1	1
Brown rat	8,082	29	104
Roof rat	20,489	21	43
House mouse	520	1	16
*44. *Hypoaspis* sp.			
Brown rat	8,082	5	5
Roof rat	20,489	1	1
*45. *Androlaelaps* sp.			
Brown rat	8,082	1	1
*46. *Gymnolaelaps* sp.			
Brown rat	8,082	1	1
Roof rat	20,489	2	2
*47. *Laelaspis* sp.			
Brown rat	8,082	1	1
Roof rat	20,489	1	11
*48. *Borinquolaelaps* sp.			
Roof rat	20,489	1	1
*49. *Lasioseius* sp.			
Brown rat	8,082	1	1
50. *Haemogamasus* sp.			
Howell mole	7	4	30
51. *Euhaemogamasus liponyssoides* (Ewing)			
Opossum	349	1	4
Howell mole	7	2	10
Cotton mouse	249	5	6
Cotton rat	966	4	5
Pine mouse	5	1	1
52. *Euhaemogamasus* sp.			
Brown rat	8,082	1	8
53. *Laelaps* sp.			
Rice rat	29	2	6
54. *Haemolaelaps geomys* Strandtmann			
Pocket gopher	1	1	148
Spotted skunk	102	1	1
55. *Haemolaelaps glasgowi* (Ewing)			
Opossum	349	31	222
Free-tailed bat	6	1	1
Cottontail	215	2	2

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
Marsh rabbit	22	1	1
Gray squirrel	101	9	11
Rice rat	29	3	13
Cotton mouse	249	50	131
Old-field mouse	243	33	91
Cotton rat	966	720	9,858
Wood rat	38	7	15
Pine mouse	5	3	21
Brown rat	8,032	90	229
Roof rat	20,489	84	127
House mouse	520	1	3
Raccoon	100	1	1
Florida skunk	110	4	6
Spotted skunk	102	2	2
56. *Haemolaelaps megaventralis* (Strandtmann)			
Opossum	349	2	3
Gray squirrel	101	30	312
Fox squirrel	42	10	135
Flying squirrel	14	1	2
Old-field mouse	243	4	8
Cotton rat	966	1	2
Brown rat	8,082	100	175
Roof rat	20,489	130	386
House mouse	520	4	6
Spotted skunk	102	2	2
57. *Haemolaelaps morlani* Strandtmann			
Brown rat	8,082	1	2
Roof rat	20,489	2	16
58. *Haemolaelaps* sp.			
Brown rat	8,082	5	5
Roof rat	20,489	9	26
59. *Eulaelaps stabularis* Koch			
Opossum	349	9	15
Fox squirrel	42	1	1
Cotton mouse	249	8	10
Old-field mouse	243	2	2
Cotton rat	966	44	98
Brown rat	8,082	18	71
Roof rat	20,489	7	7
House mouse	520	2	3
Florida skunk	110	3	15
Spotted skunk	102	3	5
60. *Echinolaelaps echidninus* (Berlese)			
Opossum	349	1	1
Brown rat	8,082	180	1,788
Roof rat	20,489	13	18
61. *Gigantolaelaps cricetidarum* Morlan			
Rice rat	29	14	46
Cotton rat	966	1	3
62. *Dermanyssus gallinae* (Degeer)			
Marsh rabbit	22	1	5

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
63. *Bdelonyssus bacoti* (Hirst)			
Opossum	349	24	206
Cottontail	215	1	1
Gray squirrel	101	2	2
Rice rat	29	11	290
Cotton mouse	249	47	326
Old-field mouse	243	5	6
Golden mouse	5	1	1
Cotton rat	966	84	183
Wood rat	38	1	4
Brown rat	8,082	1,365	14,978
Roof rat	20,489	4,756	84,276
House mouse	520	56	254
Raccoon	100	1	1
Florida skunk	110	2	2
Spotted skunk	102	1	1
Domestic cat	220	4	198
64. *Bdelonyssus haematophagus* (Fonseca)			
Little brown bat	377	1	1
Free-tailed bat	6	1	2
Cotton rat	966	1	52
65. *Bdelonyssus* sp.			
Howell mole	7	1	8
Little brown bat	377	2	4
Free-tailed bat	6	3	20
Rice rat	29	1	11
Cotton rat	966	12	85
Florida skunk	110	1	1
66. *Neoichoronyssus wernecki* (Fonseca)			
Opossum	349	34	195
Cotton rat	966	6	90
67. *Ichoronyssus quadridentatus* Strandtmann & Hunt			
Little brown bat	377	4	5
68. *Ichoronyssus robustipes* (Ewing)			
Free-tailed bat	6	1	112
69. *Ichoronyssus* sp.			
Little brown bat	377	1	1
Brown rat	8,082	1	1
70. *Steatonyssus joaquimi* Fonseca			
Little brown bat	377	2	17
71. *Hirstionyssus staffordi* Strandtmann & Hunt			
Florida skunk	110	3	10
Spotted skunk	102	13	111
Family Spinturnicidae			
72. *Spinturnix iowae* Keegan			
Little brown bat	377	5	17
Family Uropodidae			
*73. Uropoda sp.			
Brown rat	8,082	3	4
Roof rat	20,489	5	33

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
Family Ixodidae†			
74. *Ixodes bishoppi* Smith & Gouck			
Cotton rat (A—1)	966	1	1
Spotted skunk (L—1, N—2)	102	1	3
75. *Ixodes cookei* Packard			
Opossum (L—1, N—5, A—2)	349	5	8
Roof rat (N—1)	20,489	1	1
Raccoon (N—7, A—5)	100	8	12
Gray fox (L—16, N—2)	14	2	18
Weasel (L—10, N—3)	3	1	13
Florida skunk (L—48, N—176, A—121, U—1)	110	57	346
Spotted skunk (L—52, N—129, A—12)	102	34	193
76. *Ixodes scapularis* Say			
Opossum (A—7)	349	5	7
Gray fox (L—91, A—11)	14	4	102
Raccoon (A—1)	100	1	1
Weasel (U—1)	3	1	1
Florida skunk (N—2, A—2)	110	3	4
Bobcat (A—1)	3	1	1
77. *Ixodes* sp.			
Raccoon (A—1)	100	1	1
Florida skunk (L—19)	110	4	19
78. *Ixodes texanus* Banks			
Raccoon (L—5, N—19, A—26)	100	14	50
79. *Amblyomma americanum* (Linnaeus)			
Opossum (L—15, N—1)	349	2	16
Cottontail (L—14, N—101, A—3)	215	14	118
Gray squirrel (L—5, N—6)	101	3	11
Fox squirrel (N—10, A—2)	42	6	12
Brown rat (N—1, A—1)	8,082	2	2
Roof rat (L—2, N—1)	20,489	3	3
Gray fox (L—1, N—4, A—1)	14	3	6
Raccoon (L—178, N—66)	100	12	244
Florida skunk (L—14, N—28)	110	7	42
Spotted skunk (N—1)	102	1	1
Bobcat (L—7, N—8)	3	2	15
Domestic cat (U—1)	220	1	1
80. *Amblyomma maculatum* Koch			
Cotton rat (N—6, U—1)	966	4	7
Brown rat (L—1, N—5)	8,082	4	6
Gray fox (A—5)	14	2	5
81. *Amblyomma tuberculatum* Marx			
Gray fox (L—4)	14	1	4
82. *Dermacentor variabilis* Say			
Opossum (L—20, A—390, U—1)	349	71	411
Cottontail (L—15, N—81, A—91, U—28)	215	41	215
Marsh rabbit (U—1)	22	1	1
Gray squirrel (L—6, N—8, A—1)	101	7	15
Fox squirrel (L—80, A—6)	42	5	86

† Stages of Ixodidae are shown in parentheses after the mammal name with A for adults, N for nymphs, L for larvae and U for unrecorded stages.

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
Rice rat (L—126, N—19)	29	12	145
Cotton mouse (L—144, N—32)	249	51	176
Old-field mouse (L—5, N—3)	243	5	8
Golden mouse (L—2)	5	1	2
Cotton rat (L—214, N—171, U—8)	966	116	393
Wood rat (L—1, N—1)	38	2	2
Brown rat (L—188, N—48, U—5)	8,082	52	241
Roof rat (L—95, N—14, A—1, U—21)	20,489	69	131
House mouse (L—4)	520	3	4
Gray fox (L—49, A—36)	14	6	85
Raccoon (L—15, N—6, A—507, U—2)	100	43	530
Florida skunk (L—4, N—1, A—27, U—2)	110	10	34
Spotted skunk (L—3, N—1)	102	2	4
Bobcat (A—10)	3	2	10
Domestic cat (A—6)	220	4	6
83. *Haemaphysalis leporis-palustris* (Packard)			
Opossum (A—2)	349	2	2
Cottontail (L—651, N—1570, A—1152, U—53)	215	172	3,386
Marsh rabbit (L—43, N—62, A—96)	22	19	201
Cotton rat (L—1, N—8, A—6)	966	2	15
Brown rat (L—1, N—1, A—3)	8,082	5	5
Roof rat (L—6, N—3, A—2)	20,489	9	11
House mouse (L—1, N—1)	520	1	2
Gray fox (A—6)	14	2	6
Florida skunk (N—1)	110	1	1
Domestic cat (N—2)	220	2	2
Family Pyemotidae			
*84. *Pediculopsis spinosus* (Kramer)			
Roof rat	20,439	1	1
Family Raphignathidae			
*85. *Raphignathus* sp.			
Roof rat	20,489	1	2
Family Cheyletidae			
*86. *Cheyletus eruditus* (Schrank)			
Opossum	349	1	52
Harvest mouse	3	1	1
Old-field mouse	243	1	1
Wood rat	38	1	3
Brown rat	8,082	46	123
Roof rat	20,489	52	248
House mouse	520	1	1
*87. *Cheyletus malaccensis* Oudemans			
Brown rat	8,082	4	4
Roof rat	20,489	18	21
*88. *Cheyletus* sp.			
Cotton rat	966	2	2
Brown rat	8,082	2	2
Roof rat	20,489	5	5
*89. *Cheyletia* sp.			
Roof rat	20,489	6	8

TABLE 2.—(*continued*)

Ectoparasite-host list	Number of host animals: examined	infested	Number of arthropods collected
*90. *Cheyletiella parasitivorax* (Megnin)			
Cottontail	215	1	1
*91. *Cheletomorpha lepidopterorum* (Shaw)			
Roof rat	20,489	2	2
*92. *Cheletophyes* sp.			
Roof rat	20,489	1	1
*93. *Eucheyletia flabellifera* (Michael)			
Roof rat	20,489	2	2
Family Myobiidae			
94. *Radfordia ensifera* (Poppe)			
Brown rat	8,082	1	1
Roof rat	20,489	2	2
Family Bdellidae			
*95. *Scirus longirostris* Hermann			
Old-field mouse	243	1	1
Family Trombidiidae			
96 *Euschöngastia* sp.			
Gray squirrel	101	1	2
97. *Trombicula alfrèddugesi* (Oudemans)			
Opossum	349	6	23
Cottontail	215	4	12
Gray squirrel	101	3	9
Cotton rat	966	1	1
Brown rat	8,082	1	1
Roof rat	20,489	1	1
Gray fox	14	1	2
98. *Trombicula* sp.			
Cottontail	215	1	1
99. *Trombicula splendens* (Ewing)			
Opossum	349	15	106
Cottontail	215	1	2
Gray squirrel	101	6	21
Rice rat	29	1	11
Cotton rat	966	5	26
100. *Trombicula whartoni* (Ewing)			
Gray squirrel	101	10	11
Fox squirrel	42	3	3
Family Listrophoridae			
101. *Listrophorus* sp.			
Rice rat	29	8	3,576
102. *Listrophorus bakeri* Radford			
Cotton mouse	249	1	1
Cotton rat	966	68	1,901
103. *Listrophorus gibbus* Pagenstecher			
Roof rat	20,489	3	19
Family Cymbaeremaeidae			
*104. *Scapheremaeus* sp.			
Fox squirrel	42	1	1
Family Oribatulidae			
*105. *Zygoribatula* sp.			
Cottontail	215	1	1
Roof rat	20,489	1	1

TABLE 3.—Host relationships of some ectoparasites that were commonly collected in southwest Georgia during the period of October 1945-April 1949 (exclusive of any host species where less than 14 specimens were examined).

	H. hirsuta	*P. spinulosa*	*E. gallinacea*	*C. simplex*	*C. felis*	*X. cheopis*	*P. gwyni*	*L. segnis*	*H. glasgowi*	*H. megaventralis*	*B. bacoti*
Opossum	0	1	1	1	**3**	1	**3**	1	1	1	1
Little brown bat	0	1	0	0	1	1	0	1	0	0	0
Cottontail	0	0	1	3	1	0	1	1	1	0	1
Marsh rabbit	0	0	0	**3**	1	1	0	0	1	0	0
Gray squirrel	0	1	1	0	0	1	0	0	1	**3**	0
Fox squirrel	0	0	0	0	1	0	0	1	0	**2**	0
Flying squirrel	0	0	0	0	0	0	0	1	0	1	0
Rice rat	1	1	0	0	0	0	**2**	0	**2**	0	**3**
Cotton mouse	1	1	0	0	1	1	1	1	**2**	0	**2**
Old-field mouse	1	1	1	0	0	1	1	0	**2**	1	1
Cotton rat	**3**	1	1	0	1	1	**3**	1	**3**	1	1
Wood rat	1	**2**	0	0	0	0	0	0	**2**	0	1
Brown rat[4]	0	**3**	**2**	0	1	**3**	1	**2**	1	1	**2**
Roof rat[4]	0	**3**	1	1	1	**2**	1	**2**	1	1	**2**
House mouse	0	1	1	1	1	1	0	**2**	1	1	**3**
Gray fox	0	0	1	**3**	**3**	0	0	0	0	0	0
Raccoon	0	1	0	1	1	1	1	0	1	0	1
Florida skunk	0	0	1	0	1	0	1	0	1	0	1
Spotted skunk	0	0	**2**	0	1	1	1	0	1	1	1
Domestic cat	0	0	**2**	1	**3**	1	1	1	0	0	1

Legend: 0—Not infested. 1—Occasional, 0.1-9.9% of the mammals infested. 2—Moderate, 10-24.9% of the mammals infested. 3—Common, 25% or more of the mammals infested.

[4] Abundance of ectoparasites, especially *X. cheopis* and *L. segnis*, on domestic rats was reduced by extensive DDT dusting in two counties.

The Preputial Organ of Snails in the Genus Helisoma (Gastropoda: Pulmonata)*

Emile T. Abdel-Malek
University of Michigan, Ann Arbor

The structure of the penis of members of the family Planorbidae has been considered by several workers. In this family, as well as in other families of the Basommatophora and the Stylommatophora, it has been used as one of the important genital structures in taxonomic studies largely because it reveals many generic and specific relations. In the classical work on the morphology of planorbids by Buchner (1891), the penis of members of the genera *Planorbarius, Segmentina, Planorbis* and *Anisus, Bathyomphalus* and *Gyraulus* were compared. Rao (1923) and also Baker (1933 and 1945) described the penis of *Indoplanorbis* in considerable detail. Soos (1935) dealt with the genitalia of Hungarian planorbids, particularly *Anisus* (*Tropidiscus*), *Gyraulus* and *Armiger* and he, too, emphasized the importance of the penis in taxonomy.

The presence of a "penial gland" in the North American genus *Helisoma* was first reported by Baker (1926) and he also found it later in several other genera of American, European, and Asiatic planorbids. This same investigator (1931) thought that the gland was in some way involved in the formation of the spermatophore and, consequently, called it the spermatophore gland. Later, Baker realized that this assertion was not in agreement with the structure of this organ. In 1945 he stated that the function of the "penial gland" "is insufficiently known but it seemed to him that the secretion of the gland might serve to dilate an opening through which the verge protrudes or that the gland might serve as an excitatory organ or sarcobelum.

In this present study, special attention is given to the morphological and histological structure of the organ, as well as to the mating habits of the snails, in order to clarify how this gland functions. *Helisoma trivolvis* was used mainly for this work, but a comparison was also made with certain other members of this genus. Further studies on other genera will be published in a forthcoming paper.

Penial Complex

The term "penial complex" in the family Planorbidae was introduced by Baker (1931, 1945) to include a verge, a verge sac, a preputium and the muscles attached to these organs (Pl, I, D). The verge sac, the distal part of the penial complex, has a verge within it and receives a vas deferens at its globular end. The verge sac is pyriform, distinct from and confluent into

* From the Department of Zoology and the Museum of Zoology, University of Michigan, Ann Arbor.

the proximal portion, the preputium. The latter opens to the outside through the male genital opening situated at the base of the left tentacle. The preputium and verge sac are separated by a constriction which Baker (1931, 1945) called the diaphragm. A large preputial organ is found inside the preputium and is attached to its wall by a stalk shortly above the diaphragm. Through this stalk a duct passes from the organ through a depression in the wall of the preputium, becomes coiled outside the preputium and opens at the base of the diaphragm. The latter is a muscular ring with a narrow opening in its center which has an irregular boundary.

In *Helisoma trivolvis* there is no enlargement of the vas deferens before it enters the penial complex. Such an enlargement has been called an epiphallus, a term used for a larger and more conspicuous structure in land snails. In *H. anceps,* there is an epiphallus (Pl. I, A), though not so conspicuous as that of land snails.

The penial glandular organ is a large structure occupying almost all the cavity of the preputium (Pl. I, B and D). It is cup-shaped with a prominent concavity. Its typical form is best shown in the everted condition of the penial complex (Pl. II, A). In non-everted (normal) fixed specimens its shape differs slightly in several individuals of the same species and from the same locality because in the process of fixation there are varying degrees of contraction. In *H. duryi* from Florida, the penial organ is an elongated pad-shaped structure, as demonstrated in the everted penial complex (Pl. II, B). Within the concavity of the penial organ there are several longitudinal folds which are continuous with others on the surface. The stalk which connects the organ to the wall of the preputium is thick and short in fixed specimens, but it can be considerably extended when it is erected during mating.

HISTOLOGY OF THE PREPUTIAL WALL AND PREPUTIAL ORGAN

The inside of the preputial wall is lined with an epithelium formed of short columnar cells which are almost cuboidal and are underlain by a connective tissue layer in which a large number of muscle fibers are arranged longitudinally and circularly. These fibers appear to dominate considerably the connective tissue fibers (Pl. I, C). In this layer there are a number of elongate pigment cells which give the preputial wall its characteristic dark grey color. This wall is covered on the outside by a thin squamous epithelium. The inner epithelium of the wall shows a number of furrows and undulations.

The preputial organ is almost round in transverse section. It is surrounded by an epithelium formed of cuboidal to short columnar cells. This same epithelium is invaginated in several areas and becomes continuous with the main glandular epithelium in the center of the organ. The latter epithelium (Pl. I, C) is folded in a compound tubular arrangement; its cells are of the long columnar type containing basal nuclei. The tubules are very much branched in such a way that the cavity is reduced considerably. A large numbe

of cells in the central epithelium are secretory but no mucous-secreting cells are found among them. However, a number of cells in the epithelium lining the penial organ, especially at the entrance of the passages leading to the central branched epithelium, secrete mucous as is indicated in the manner in which they take a very light purple color with thionin. From the glandular epithelium the secretion is carried to the surface of the organ through the passages or canals. The secretion is also carried to the diaphragm and the neighboring part of the verge cavity by means of the long, coiled duct found just outside of the preputium.

The epithelium surrounding the penial organ itself lies on a very thin basement membrane underlain with a well-developed zone of compact, longitudinal, followed by circular, muscle fibers. Between this layer and the central branched glandular epithelium is a layer of connective tissue with longitudinal and radial muscle fibers. This layer also contains many blood spaces. The rich blood supply can be recognized during mating when this organ appears to be highly vascular. There is reason to suppose that both the large amount of muscle tissue, as well as the action of the blood in the blood spaces of this preputial structure, are largely responsible for its contraction and extension.

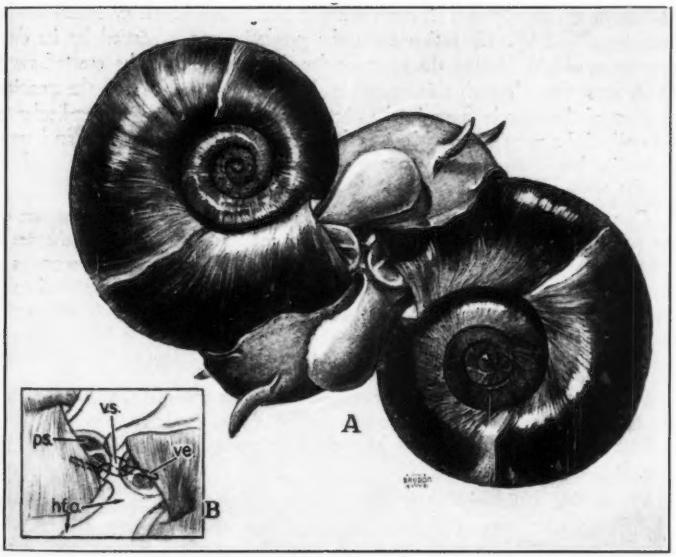
In the connective tissue layer there are also a number of elongate, dark pigment cells and a number of spherical crystalline structures. Similar "incrustations" were reported by Hubendick (1948) to occur in the penis of some species of *Bulinus*. In the present study it was observed that these incrustations also occur in other parts of the genitalia as will be considered in more detail in another publication. Other parts of the snail also contain similar concretions usually in connective tissue and apparently because of the presence of blood spaces. It was noticed that these masses occur in large numbers during estivation and hibernation. It seems possible that they are the result of the accumulation of excretory matter of some sort.

The wall of the duct of the preputial organ consists of a columnar epithelium lining the cavity and is underlain by a connective tissue layer which has a large number of circular muscle fibers. There are also a number of longitudinal muscle fibers underneath a squamous epithelium which surrounds the wall on the outside.

MATING HABITS

In mating, attention is called to the fact that a process of *eversion* of the penial structures is involved, i.e., a process of bringing the structures inside the penial complex to the outside. Before mating, the snail is seen crawling on its partner's shell until the foot adheres firmly partly to the right and partly to the left side of the shell. The preputium is then everted and the preputial organ is seen outside the male opening, appearing as a tactile organ. After locating the structures in this area the organ gets hold of the "neck" of the same snail. In the region slightly beyond the mantle collar and on the right and ventral sides of the neck, the preputial organ acts as a hold-fast

organ (Text Fig. 1A). It has the form of a disc of mushroom shape (Pl. II A) and operates as a sucker utilizing both its folds and the secretion exuded from the surface of these folds. Once the organ gets hold of the slightly twisted neck of the same snail the verge is seen protruding through the opening in the center of the diaphragm in an attempt to go through the vagina passing underneath the pseudobranch (Text Fig. I B). The preputial structure or the "hold-fast organ," a term suggested by the writer, looks highly vascular when everted and also during mating. Accordingly the color of the organ is dark red giving a distinctive appearance as compared to the verge sac and the neighboring structures. While adhering to the right and ventral surfaces of the neck, the hold-fast organ is in a process of continuous slow pulsation at the rate of 13 to 15 times per minute. However, the verge and the verge sac are on the opposite side underneath the pseudobranch of the partner. In contrast to the hold-fast organ, the verge sac does not show noticeable movement, while the verge itself shows occasional slight contraction and relaxation. Cases where a snail functions only as a female and its partner as a male were observed and the preputial organ assumes the same function and position.



Text fig. 1.—A. Illustration showing two copulating specimens of *Helisoma trivolvis*, each individual acting both as a male and as a female. They adhered firmly to each other for almost 5½ hours. The two verge sacs are partly overlapping. B. A semidiagrammatic drawing to show the area between the two snails. Dotted lines indicate portions of verge sacs and verges underneath the pseudobranchs.

DISCUSSION

The above observations permit certain conclusions concerning the function of the so-called "preputial gland." The "gland" is a hold-fast organ which functions while the snail is mating. It should be emphasized that the organ adheres to the neck of the same snail and therefore acts as a brace and helps to produce leverage. Also, by pushing the twisted head-foot region aside it provides enough space for the verge to extend underneath the pseudobranch to enter the vagina. The adhesion of the foot of one snail to the shell of the partner (Text Fig. 1A) provides a complete attachment of both individuals to one another and, therefore, also secures the process of mating. An indication of how complete this adhesive process is during copulation is shown by the fact that two snails still joined together may sometimes be seen floating and moving around. In part the secretion from the hold-fast organ helps in fastening it to the neck of the same snail and this union is also secured by the suction produced by the cup-shaped end with its concavity and folds.

Another function of the preputial organ involves the aperture located in the center of the diphragm. In *Helisoma trivolvis* the duct from the organ passes through this diaphragm and opens at its base (Pl. IB). Moreover, in *H. anceps* the duct passes through the wall and opens at the periphery of the aperture (Pl. IA). Secretion from the preputial organ carried by its duct appears to aid in dilating the aperture for the reception of the erected verge which must pass through this opening. Dilation is promoted by the position of most of the muscle fibers in the diaphragm since they are perpendicular to the wall of the preputium. Usually this opening is narrow and has an irregular outline but when the verge passes through it the aperture attains a uniform circular outline with a diameter slightly more than that of the verge.

One might assume at first that secretion from the glandular epithelium of the preputial organ carried to the verge sac renders the latter and the verge inside it moist. However, the inner epithelium of the verge sac contains a large number of flask-shaped glandular cells which apparently provide the verge sac with its needed secretion. Consequently, it appears evident that the secretion from the preputial organ is not used for lubricating the verge sac but for helping in the dilation of the aperture in the diaphragm.

In the steps preparatory to mating the hold-fast organ acts as a tactile organ. If it were not for its large size and its characteristic cup-shaped end, it might be mistaken for a tentacle because of its particular movements.

Baker (1945), who had not observed the function of the preputial organ during mating, believed that it might be an excitatory organ or sarcobelum. This latter term was used by Taylor (1900) and it corresponds to the German term "Reizkorper," and the French expression "organ excitateur" which is ususally a male excitatory organ. Both from observations of mating snails, as well as from a study of sagittal and transverse sections of the penial complex of some species of *Helisoma*, it becomes necessary to reject the claim that the structure found in the preputium of snails of this genus is an excita-

tory organ. In *Helisoma trivolvis* (Pl. IB) and *H. anceps* (Pl. IA) there is a fleshy papilla at the end of the verge. In *H. anceps* the length of the papilla is about three times that of *H. trivolvis*. The papilla is of the same structure as the verge though more muscular and contains a hard fibrous area near its tip (Pl. IB and Pl. IIE). This hard portion can be seen in gross examinations (Pl. ID), and was considered to be the seminal opening by Baker (1931, 1945). However, in sections it is clear that the seminal opening is located at the base of the papilla at a considerable distance from its tip, especially in *H. anceps*. Excitation of the partner is, therefore, promoted by this papilla and if the preputial organ does take part in excitation when it is first protruded following eversion of the preputium, that function is not conspicuous.

SUMMARY

This study reveals the function of a structure containing glandular elements and is present in the preputium of snails in the genus *Heliosma*.

Observations on mating showed that the penial complex of the snail is everted in order that the process of mating becomes possible. While the snails are mating the preputial organ functions as a hold-fast organ, adhering firmly to the neck of the *same* snail thus acting as a brace and helping to produce leverage. Also, by pushing the twisted head-foot region aside it provides a space for the verge to reach the vagina.

A large number of flask-shaped cells present in the epithelium lining the verge sac provide the latter and the verge with their needed secretions. Consequently, secretions from the compound tubular glandular epithelium of the preputial organ have little or no effect on rendering these structures moist but, apparently help in dilating the aperture in the center of the diaphragm, and in keeping it moist.

The view that the preputial organ is a sarcobelum is rejected since sections in the penial complex revealed that in spite of the presence of that organ in the preputium there is a papilla at the end of the verge and has a hard fibrous area at its tip. This papilla functions as an excitatory organ.

The term "hold-fast organ" is suggested to replace the term "preputial gland."

ACKNOWLEDGMENTS

Appreciation is expressed to Dr. Henry van der Schalie of this Department and to Dr. Elmer G. Berry of the Division of Tropical Diseases, National Institutes of Health, Bethesda, Maryland, for advice and encouragement. The author also wishes to thank Mr. William Brudon, artist at the Museum of Zoology, for drawing Text Figure 1 and for advice concerning the plates.

REFERENCES

BAKER, F. C. 1926—Nomenclatorial notes on American fresh-water Mollusca. Trans. Wisconsin Acad. Arts, Sci. and Lett. 22: 192-205.

———1931—The classification of the large planorbid snails of Europe and America. Proc. Zool. Soc. London 1931(2): 575-592.

———1933—The genitalia of the Indian mollusk *Indoplanorbis exustus*. Jour. Morph. 55: 1-13.

———1945—The molluscan family Planorbidae. Univ. Illinois Press. Collation, revision and additions by H. J. vanCleave, 530 pp.

BUCHNER, O. 1891—Beiträge zur Kenntnis des Baues einheimischer Planorbiden. Wurt. Naturw. Jahresh. 47: 35-118.

HUBENDICK, BENGT. 1948—Studies on *Bulinus*. Arkiv för Zoologi, Stockholm 40(A): 1-63.

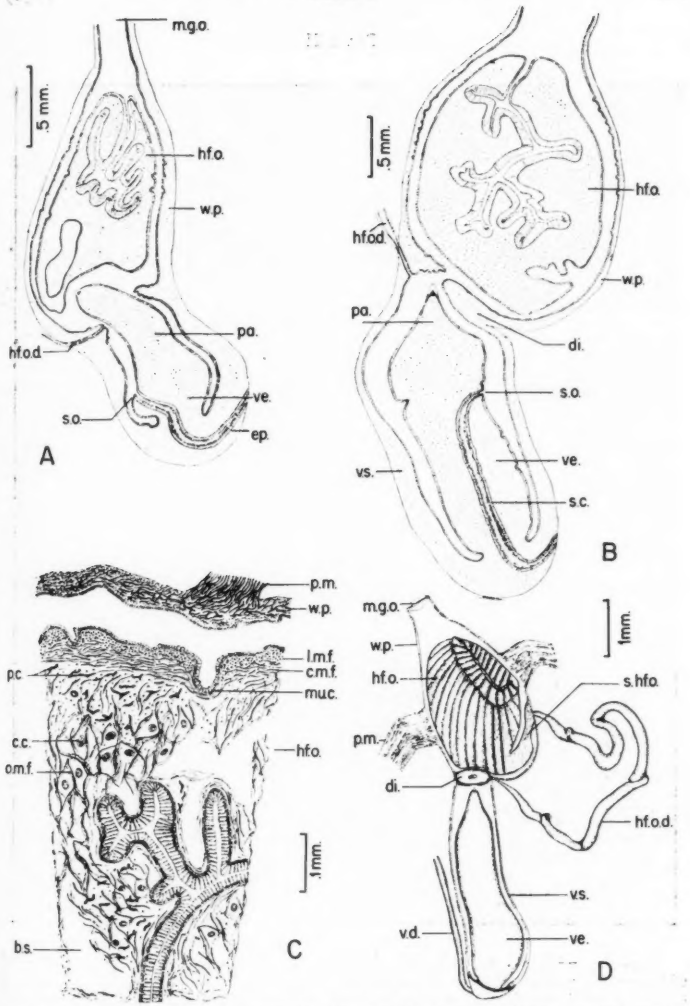
RAO, H. SRINIVASA. 1923—On the anatomy of *Indoplanorbis exustus* (Mollusca, Pulmonata). Rec. Indian Mus. 25: 199-219.

SOOS, A. 1935—A Magyarországi Planorbis-Félék warkészülékének Alak-és Szövettana. Állattani Közlémények 32 Kötet: 21-42.

TAYLOR, J. W. (1894-1900)—Monograph of the land and fresh-water mollusca of the British Isles. Structural and general volume. Leeds, pp. 454.

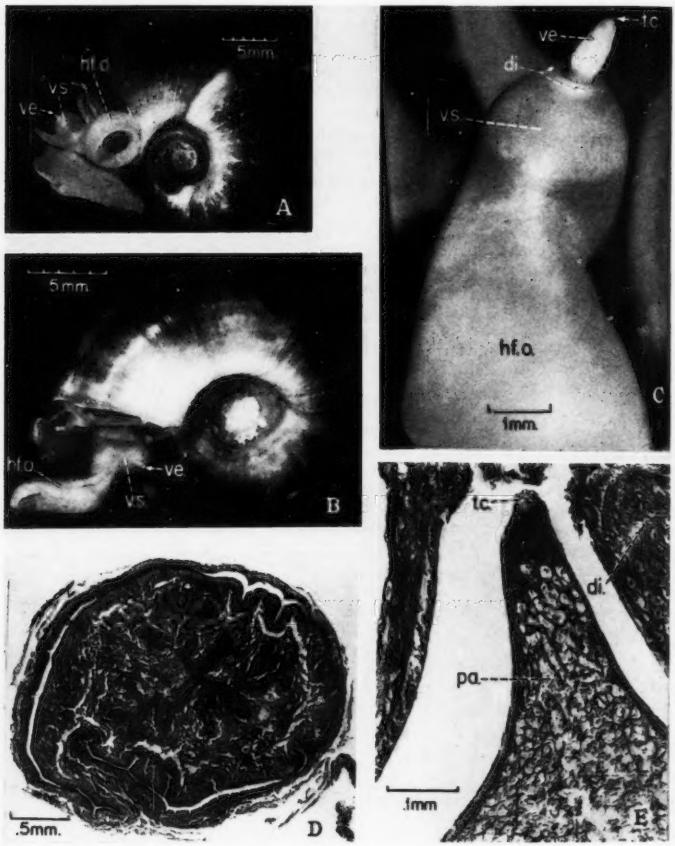
EXPLANATION OF PLATES

ABBREVIATIONS: b.s.—blood space, c.c.—crystalline concretion, c.m.f.—circular muscle fiber, di.—diaphragm, ep.—epiphallus, hf.o.—hold-fast organ, hf.o.d.—hold-fast organ duct, l.m.f.—longitudinal muscle fiber, m.g.o.—male genital opening, mu.c.—mucous cell, pa.—papilla, p.c.—pigment cell, p.m.—penial muscle, o.m.f.—oblique muscle fiber, s.c.—seminal canal, s.hf.o.—stalk of hold-fast organ, s.o.—seminal opening, t.c.—transparent cap, v.d.—vas deferens, ve.—verge, v.s.—verge sac, w.p.—wall of preputium.



Figs. A-D.—A. Schematic composite drawing of four neighboring sagittal sections through the penial complex of *Helisoma anceps*. Heidenhein's iron hematoxylin preparation. Papilla is considered that part of the verge beyond the seminal opening and has a dark fibrous "stylet" near its tip. B. Same as A, but in *H. trivolvis*. C. Portion of a transverse section through the preputium of *H. trivolvis* showing the preputial wall and the hold-fast organ. D. Penial complex of *H. trivolvis* opened to show hold-fast organ and verge.

PLATE II



Figs. A-E.—A. *H. trivolvis* from Michigan fixed with the penial complex everted while mating; notice sucker-like shape of hold-fast organ. B. *H. duryi* from Florida fixed with the penial complex everted; notice difference in the shape of the hold-fast organ from that of *H. trivolvis*. C. Everted penial complex of *H. trivolvis* enlarged; transparent cap above hard stylet is shown at the tip of the verge. After eversion, the opening in the center of the diaphragm becomes the functioning male aperture through which the verge protrudes. D. Transverse section through the preputium of *H. trivolvis* to show hold-fast organ attached by a stalk to the preputial wall. E. Parasagittal section through the papilla at the end of the verge of *H. trivolvis* to show fibrous zone near its tip. The small area (t.c.) covering this fibrous zone is transparent in gross examination.

Records and Flower Preferences of Masarid Wasps. II. Polytropy or Oligotropy in Pseudomasaris? (Hymenoptera: Vespidae)

Kenneth W. Cooper

Department of Biology, Princeton University, Princeton, New Jersey

New distributional records for nine species of masarid wasp belonging to the endemic North American genus *Pseudomasaris* have been presented in an earlier report (Cooper and Bequaert, 1951) which, in addition, summarized new records of flower visits by seven species. It is the intent of this paper to describe observations on flower visits and to review and discuss critically what is now known of the flower preferences of the three species, *Pseudomasaris vespoides* (Cresson), *Ps. marginalis* (Cresson) and *Ps. zonalis* (Cresson), that are known to occur in Colorado. It will be shown that certain earlier published records, which would lead to the conclusion that *Ps. vespoides* has a very wide range of flower hosts (i.e., is polytropic), are open to very considerable doubt. It may well indeed turn out that this wasp is *oligotropic*, since the only unquestionably reliable records currently at hand suggest that it has only a very limited range of preferred flowers (at least in Colorado), and restricts its attention almost wholly to certain species of *Penstemon*. At any rate, *Pseudomasaris vespoides*, and possibly other *Pseudomasaris* species, are on the whole relatively oligotropic. *Ps. vespoides* in Colorado, for example, has its pollen- and nectar-gathering niche within the deep-throated corollas of larger beard-tongues.

It is hoped that the evidence and discussion presented here, since neither is final, will encourage the collection of field notes with a view to settling the matter, for the evolutionary significance of such oligotropy is very considerable. A not unexpected finding may be different flower spectra in different areas, reflecting population diversities within the species' range.

The Flower Preferences of Coloradan Pseudomasaris.—Bequaert (1940) has given a detailed review of the known flower preferences of masarid wasps. Of foreign genera, *Jugurtia*, *Celonites* and *Masaris* apparently contain species whose normal plant visits include members of at least two or more plant families. On the other hand all species of *Quartinia* for which there are records seem to prefer composites to the exclusion of other flowers. To judge from most existing records it seems very likely that American wasps of the genus *Pseudomasaris* almost exclusively visit Scrophulariaceae (*Penstemon*, and perhaps *Besseya*) and hydrophyllaceans (*Phacelia* and *Eriodictyon*). But there can be no doubt as to the predilection of *Pseudomasaris vespoides* for flowers of *Penstemon*.

Ps. vespoides has, for example, been previously recorded as visiting not

less than nine species of *Penstemon*,[1] and at least three of these (*Ps. acuminatus*, *P. comarrhenus* and *P. glaber*) are said to attract the wasp in Colorado. But *Penstemon acuminatus* and *P. glaber* do not occur (or are perhaps very rare) in central Colorado (v. Pennell, 1920), and so are almost certainly based on misidentifications. According to Dr. William Weber, authority on the flowering plants of Boulder County, Hicks' (1929) record of *P. acuminatus* should be referred to *P. secundiflorus* which is in bloom in late May. The *Penstemon glaber* record from Teller County almost certainly represents captures of the wasp at *P. alpinus*, for in Central Colorado *alpinus* is very commonly mistaken for *glaber*. Adding to these the records of Cooper and Bequaert, Coloradan *Pseudomasaris vespoides* are known to frequent the flowers of at least *Penstemon alpinus*, *P. comarrhenus*, and *P. unilateralis*, and probably also *P. secundiflorus*. Of these, the first three fall in the section *Glabri* of *Penstemon*, while *secundiflorus* is a member of the section *Coerulei*.

In this connection, it is interesting that two of the remaining six species of *Penstemon* known to be frequented by *Pseudomasaris vespoides* elsewhere are also members of the section *Glabri* (*i.e.*, *P. payetensis* and *P. cyaneus*), both having been recorded by Pennell (in Bequaert, 1940). Farther to the West, representatives of the sections *Saccanthera*, *P. azurea*, *P. venustus* (Pennell, in Bequaert 1940) and *P. heterophyllus* (Hicks, 1929), and *Spectabiles*, *P. spectabilis* (Davidson, 1913), are visited. The important point would appear to be that all of these *Penstemon* have large flowers of quite similar form, and although the wasp seems to be oligotropic in the sense that it appears to be restricted to *Penstemon*, it accepts quite a wide choice within *Penstemon*, frequenting as it does members of at least four of the nineteen or more sections of this large genus.

Even though *Pseudomasaris vespoides* does, at one time or another, frequent several species of the larger *Penstemon*, it would seem that at a given time, and in a given locality, it may show a marked preference for one species and disregard others. At Rainbow Lakes, Colorado, along the broad road margin near the public camp site, three species of *Penstemon* were abundant in 1949, making a very large mixed population of flowers. These occurred in the very approximate ratio of 1 *P. procerus*:20 *P. whippleanus*:400 *P. alpinus*. The hydrophyllacean, *Phacelia heterophylla*, was scattered through the stand at a frequency about the same as that of *P. whippleanus*. Now, despite the fact that *Ps. vespoides* was very common here (many more than the 13 recorded in Cooper and Bequaert could have been collected), the wasp was observed through the morning and afternoon to visit only *Penstemon alpinus*. Both *Pseudomasaris zonalis* and *Ps. marginalis* were also present, and these, without exception, attended only *Phacelia heterophylla*. Both males and females of all three masarids visited only the flower preferred by the

[1] Records in Cooper and Bequaert (1951) and in Bequaert (1940), but omitting those in the latter paper of *Penstemon glaucus* (= *whippleanus*), *P. gracilis*, and *P. secundiflorus*, all of which were cited from Clements and Long (1923). Reasons for omission of records from Clements' and Long's work is discussed in detail in the final section of the present paper.

particular species in the mixed stand, and, in the case of *Ps. vespoides*, they would climb wholly within the flower on alighting. (Such is not possible for *Ps. marginalis* and *Ps. zonalis* visiting *Phacelia*, because the scorpion weed has a relatively short corolla.) Males of each species frequently flew to their preferred plant, apparently inspected it without alighting, then hovered near the plant, ultimately alighting on the ground below with wings and antennae prettily spread.

Flower visits continued, perhaps less frequently, during cloudy spells and the wasps were still active at 5 PM when observations were ended. Very likely at least some *Ps. vespoides* spend the night within their chosen flowers. For example, two female *Pseudomasaris vespoides* collected within the corollas of *Penstemon alpinus*, at 11:20 AM, in the vicinity of Science Lodge, Colorado, Aug. 13, were apparently "asleep" there, and not feeding. It was a very cold, raw and cloudy morning, and no wasps had been found flying all morning. The masarids were in laterally adjacent flowers of one plant, and when removed were very torpid, remaining quiescent with wings folded, antennae back, and abdomen curled forward until the warmth of the hand brought them to activity.

The only exception noted to a strict preference for *Penstemon alpinus* on the part of *Ps. vespoides* was at a mixed but scattered stand of *P. alpinus* and *P. unilateralis*, in a ratio of approximately 20:1 respectively, growing along the roadside perhaps three-fourths of a mile from the camp site at Rainbow Lakes. Here one male of *Ps. vespoides* was caught within a flower of *P. unilateralis*. Unfortunately no other *Ps. vespoides* were seen here, and so the interesting question as to whether the wasp would visit both species of *Penstemon* in the mixed stand, or only *P. unilateralis*, remains unanswered.

If *Pseudomasaris vespoides* visits *Phacelia*, it is probably rarely (see below). At Gold Hill, Colorado, in 1949 and again in 1950, *Phacelia heterophylla* was assuredly a hundred fold as common as *Penstemon alpinus*, yet *Ps. vespoides* was found visiting *P. alpinus* alone. Once again, *Ps. zonalis* was found only at the *Phacelia*. Indeed at no time was either *Ps. zonalis* or *Ps. marginalis* seen to evince interest in species of *Penstemon* or indeed any flower other than the scorpion weed *Phacelia heterophylla*.

Finally, it may be of value to mention also that very considerable numbers of *Penstemon gracilis*, *P. whippleanus* (= *glaucus*) and *P. virens* were searched in the general vicinities of Nederland, Hill's Mill and Ward, Colorado, but no masarids were found at any of them. Both *Phacelia denticulata* (very few plants) and *Ph. leucophylla* were also watched for masarids, but unlike *Ph. heterophylla* seemed unattended by masarid wasps in the regions where these *Phacelia* species occurred.

Considering now the records so far treated, as well as those in Bequaert (1940) and in Cooper and Bequaert (1951), *Pseudomasaris* species would appear to be relatively oligotropic, for the most part restricting their flower preferences to single genera, or closely related genera, within one or two families of plants. From the known observations it appears that the three larger species of *Pseudomasaris* (*vespoides*, *occidentalis* and *wheeleri*) fre-

quent certain *Penstemon* species, while the other, smaller species favor *Phacelia*. On the other hand *Eriodictyon*, the only other genus of plants that is established with certainty as a host of *Pseudomasaris*, attracts both large and small species. Thus *Ps. phacelia*, *Ps. marginalis*, *Ps. zonalis*, *Ps. texanus* and *Ps. rohweri* have been recorded from species of *Phacelia*, *Ps. coquiletti* and *Ps. edwardsii* have been taken at *Eriodictyon* and *Phacelia*, and *Ps. wheeleri* has been collected at *Eriodictyon* and *Penstemon*.

It is an interesting fact that to date no *Pseudomasaris* species is known to visit both *Penstemon* and *Phacelia*. As the flowers of *Penstemon* are noticeably larger than those of *Phacelia*, the correlation in size of visitor and preferred flower is evident. Yet the significance (and possible origin) of this preference is by no means clear. While the larger *Pseudomasaris* may be effectively barred by size from the small *Phacelia* flowers (if, for one reason or another, entrance to the flower is necessary for the wasp to feed), there would seem to be no obvious impediment to the smaller *Pseudomasaris* entering the large *Penstemon* flowers. It should be noted on this score that neither *Penstemon* nor *Phacelia* flowers have any special structures calling for particular "skill" in reaching the pollen or the nectar. Indeed, as is well known, both are visited by a fairly large variety of Hymenoptera, Diptera and other insects.

While it is clear that *Pseudomasaris vespoides* favors a fairly large number of *Penstemon* species, it is unfortunate that records are not really extensive for any other species of *Pseudomasaris*, but it may be expected that those visiting *Phacelia* will also prove to attend more than one species of scorpion weed. Thus *Ps. coquilletti*, in addition to visiting *Eriodictyon crassifolium*, also attends *Phacelia californica* and *Ph. ramosissima*, and *Ps. marginalis* is known to visit both *Ph. heterophylla* and *Ph. sericea*.

A note on Clements' and Long's records.—Despite the existence of flower records for at least eight species, it is nevertheless an open matter whether American *Pseudomasaris* have still wider flower preferences, for they occur mostly in regions where a very large flower choice is possible. It is true that the little known *Ps. texanus* has been recorded from a "plum" by Cockerell (as *Ps. albifrons* Rohwer), and from *Astragalus* by C. F. Baker (as *Ps. neomexicanus* Rohwer, see Bequaert, 1940), but *Ps. vespoides* would by all odds be the most probably polytropic species in the genus to judge from Clements' and Long's (1923) work. As considerable interest attends the question as to how wide a taxonomic spectrum of plants may be visited by each species of *Pseudomasaris*, and since other collectors have recorded *Ps. vespoides* virtually only from *Penstemon*, a rather extensive discussion of Clements' and Long's records for this wasp is now warranted. It will become evident that it is desirable and right to omit nearly all of their records from current lists of the flower preferences of this wasp, even though it may ultimately prove to be the case that *Ps. vespoides* is, in fact, polytropic as their claims suggest.

Clements and Long, it should be remarked, were concerned with the normal pollinating activities and floral preferences of insects generally, as well

as with the floral factors of importance in attracting the insects. Not only did Clements and Long study visits to the flowers under normal conditions, but they also analyzed floral factors by mutilation experiments, by supplementing floral characters with colored paper petals, honey, perfume, and so on, and by placing plants (by transplant or bouquet) in competition with one another for insect visitors. These studies were made on a fairly large scale, and were mostly carried out in a period from approximately mid-June through mid-July, to judge from the dates they cite.

At the close of Clements' and Long's work there are summary lists of "pollinators and flowers visited" and of "flowers and their visitors." For many if not most of the records it is neither clear what evidence there was at hand to classify the insect as a pollinator, nor what is to be understood by a "visit." In the summary lists *Pseudomasaris vespoides* is listed as a pollinator of some ten plants which, excluding three species of *Penstemon*, include a geranium (*Geranium caespitosum*), a borage (*Mertensia "sibirica,"* very probably *M. ciliata*), a horsemint (*Monarda fistulosa*), and members of the rose family including *Prunus* and *Rubus*. During the summers of 1949 and 1950, in the Boulder and adjacent quadrangle areas, these common plants and their close relatives were closely observed wherever found in flower, over an altitudinal range from the foothills (*ca.* 5,500 ft.) to above Summit Lake on Mt. Evans (*ca.* 13,000+ ft.). No masarid wasp was found attending any of them, or any member of the genera or families concerned, even in the montane localities where all three Coloradan species of *Pseudomasaris* are frequent. Just what significance is to be attributed to Clements' and Long's records becomes something of a puzzle, then, both in view of the collecting experiences of others and the failure of these specific, albeit brief, attempts to corroborate them. Assuredly their records are not to be explained as visits by the wasp to normally ignored flowers during the early season when *Penstemon* flowers are scarce or rare, for at least four species of *Penstemon* (including *P. alpinus* and *P. unilateralis*) are in bloom during the periods of their records, *i.e.*, from mid-June through mid-July.

It must be admitted that it does not seem to be known, at the present, whether the flowers at which *Pseudomaris* have been caught are in fact the very hosts from which they provision their nests with pollen. It might be argued that the flowers mentioned by Clements and Long are pollen providers, whereas the *Penstemon* and hydrophyllaceans supply nectar or something perhaps merely attractive to the adult wasp and not necessarily used in nest provisioning. But as *Pseudomasaris* have been recorded during their nesting season almost exclusively from *Penstemon*, *Phacelia* and *Eriodictyon*, according to the species of wasp, it seems very likely that these are the very flowers that normally provide the pollen.[2]

---

[2] Hicks (1927) does state that pollen from the nest of *Pseudomasaris vespoides* was identified as originating from some member of the Compositae. The predilection of this wasp for *Penstemon* was apparently unknown to Hicks at that time, and so it appears that the very necessary comparison of nest pollen with *Penstemon* pollen was not made. His later papers (1929, 1931) make no further claim regarding this matter.

Now if Clements' and Long's summary lists be checked against their text, several significant points emerge. For one thing, Clements and Long unfortunately fail to distinguish observations under natural conditions from those of competition or other experiments in these lists. Obviously such a distinction is of considerable importance when the normal ecology of *Pseudomasaris vespoides* is being considered. Furthermore they made what appears to be unexplained choices among their records for inclusion in their summary lists. For example, even though visits of *Ps. vespoides* (under either natural or experimental conditions) to flowers of *Mertensia pratensis* (= *franciscana* of current literature), *Penstemon secundiflorus*, *Scrophularia nodosa* and *Frasera speciosa* are recorded in the text, these unaccountably do not establish records in the summary lists of pollinators or of flowers visited. Conversely, *Pseudomasaris vespoides* is recorded as a pollinator of *Monarda fistulosa*, *Mertensia sibirica* (probably *M. ciliata* of current literature), and *Penstemon glaucus* (= *whippleanus*) in the summary lists, even though no mention of these records occurs in the text.

If flowers be excluded from further consideration for which no records are given in the text (*i.e.*, *Monarda fistulosa*, *Penstemon glaucus*), or for which text records are only of "visits" made by the wasp in competition or other experiments (*viz.*, *Rubus strigosus*, *Prunus demissa*, *Opulaster opulifolius*, *Frasera speciosa*, *Calochortus gunnisoni*, *Scrophularia nodosa*), then but six plants recorded in text or summary list need be further considered as flowers normally visited by *Pseudomasaris vespoides*. Indicating by bracketted numbers the natural visits recorded, these six plants are: *Mertensia pratensis* (= *M. franciscana*) (1), *Geranium caespitosum* (2), *Rubus deliciosus* (3), *Penstemon secundiflorus* (1), *P. gracilis* (6), and *P. glaber* (146). As pointed out earlier, records of *Penstemon glaber* from central Colorado are assuredly to be accredited to *P. alpinus*. There is then, a surprisingly large number of visits to *P. alpinus* as compared with those to other plants; surprising, that is, only if it be contended that *Ps. vespoides* is polytropic. But are the above flowers allegedly infrequently visited to be adjudged clean-cut records assignable to *Ps. vespoides?*

It is likely that, in some of these cases at least, if not all, *Pseudomasaris vespoides* and another wasp or a syrphid fly have been confused. *Geranium caespitosum* and species of *Rubus* are commonly visited by *Dolichovespula arenaria* and other vespines in Colorado, as well as by large syrphids, so it is quite possible that Clements and Long confused one or more species of *Dolichovespula*, *Vespula*, or syrphid with *Ps. vespoides*. Such a confusion with a vespine, at least, is indeed very likely for, as Bequaert (1940) has already pointed out, Clements and Long refer to "*Vespa germanica*" in portions of their text where, to judge from associated tables, they presumably intend *Ps. vespoides* (and *vice versa?*).

Furthermore, in most cases it is difficult to guess just what Clements and Long meant by a "visit." This is particularly pointed up by their inclusion in the summary lists, for example, of the predatory asilid fly *Dasyllis* as a

"pollinator" of both *Calochortus* and *Chamaenerium*. Perhaps some of the "visits" recorded by Clements and Long, if in fact by *Pseudomasaris vespoides*, took the form of the wasp flying abruptly to the flower, then hovering in flight before it, only to dash away without alighting upon the blossom. Near Science Lodge *Ps. vespoides* was once seen to do just this, a large purple aster being the object of momentary interest. Hicks (1929) also records observing that a female of *Ps. vespoides* "flying over *Argemone* sp., a wild white poppy, appeared ready to alight on it but soon flew away without doing so." Such "visits" may well have also served as basis for the records by Cockerell and Baker of *Ps. texanus* at "plum" and *Astragalus* mentioned above, but this can only be conjectured. Those cases where a plant was seen to be "visited" but two or three times under natural conditions may be mentioned as specific instances in Clements' and Long's work where such flying "visits" are quite possibly the basis for their records.

If, then, only those records where four or more instances of "visits" under normal conditions be considered, we are faced only with the records for *Penstemon alpinus* and *P. gracilis*. It is hardly possible to believe that well over a hundred visitors to *P. alpinus* are to be accredited to misidentified vespines, especially since *P. alpinus* is a definitely established host plant for *Pseudomasaris vespoides*. But it is by no mean so difficult to believe that the six *P. gracilis* records could be in error. When all is said and done, so very many uncertainties exist that the general impression with which the critical reader is left must be that Clements' and Long's records (excepting those of *Penstemon alpinus*) should be omitted from current and future lists[3] until naturalists in suitable localities make an effort to check the behavior in nature of *Pseudomasaris vespoides* with regard to the plants specifically mentioned in their text.

ACKNOWLEDGMENT

Many thanks are due Professors Robert Prettyman and J. Frank Cassel, botanist and zoologist respectively in charge of courses at Science Lodge, for their help and interest in the fieldwork. I am also grateful to Dr. Francis W. Pennell of the Academy of Natural Sciences, Philadelphia, Pa., for validating the identifications and giving advice regarding the Colorado *Penstemon* species mentioned in this and the earlier paper. Dr. William Weber very kindly gave his help with the puzzling record of *Penstemon acuminatus* from the campus of the University of Colorado.

SUMMARY

New flower records, and a re-evaluation of published records, show that *Pseudomasaris vespoides* visits at least: *Penstemon alpinus, P. comarrhenus, P. cyaneus, P. payetensis*, and *P. unilateralis* of *Penstemon* section *Glabri; P. venustus, P. heterophyllus* and probably *P. azureus* of the section *Saccanthera;*

[3] If they are not to be omitted, then *Scrophularia nodosa* and the gentian, *Frasera speciosa*, should be appended to Bequaert's (1940) listings for *Pseudomasaris vespoides* that are accredited to Clements and Long.

P. spectabilis of the section *Spectabiles;* and probably also *P. secundiflorus* of the section *Coerulei.* The general problem of relative oligotropy in species of *Pseudomasaris* is briefly discussed. Clements' and Long's records indicating wide polytropy in *Pseudomasaris vespoides* are critically examined, and reasons are given for omitting them from current lists. It would appear that most species of *Pseudomasaris* are relatively oligotropic, visiting but few kinds of strongly preferred flowers.

REFERENCES

BEQUAERT, J. 1940—Notes on the distribution of *Pseudomasaris* and on the foodplants of the Masaridinae and Gayellinae (Hymenoptera, Vespidae). Bull. B'klyn Ent. Soc. 35: 37-45.

CLEMENTS, F. C. AND F. L. LONG 1923—Experimental pollination. An outline of the ecology of flowers and insects. Carnegie Inst. Wash. Pub. 336: vii+274 pp.

COOPER, K. W. AND J. BEQUAERT 1951—Records and flower preferences of masarid wasps (Hymenoptera: Vespidae). Psyche 57(4): 137-142.

DAVIDSON, A. 1913—*Masaria vespoides.* Bull. So. Cal. Ac. Sci. 12: 17-18.

HICKS, C. H. 1927—*Pseudomasaris vespoides* (Cresson), a pollen provisioning wasp. Can. Ent. 59: 75-79.

———1929—*Pseudomasaris edwardsii* Cresson, another pollen provisioning wasp, with further notes on *P. vespoides* (Cresson). Ibid. 61: 121-125.

———1931—Notes on pollen-user wasp, *Pseudomasaris edwardsii* Cresson. Bull. So. Cal. Ac. Sci. 30: 23-29.

PENNELL, F. W. 1920—Scrophulariaceae of the Central Rocky Mountain States. Contrib. U. S. N. M. 20: 313-381.

The Ant Larvae of the Subfamily Ponerinae — Part I[1]

George C. and Jeanette Wheeler
Department of Biology, University of North Dakota, Grand Forks

Tribe Myrmeciini Emery

Genus Myrmecia Fabricius

Not differentiated into neck and body; elongate, terete and rather slender; diameter diminishing gradually from the fifth abdominal somite to the anterior end; anterior half strongly curved. Body hairs short, simply, slightly curved. Head very small; cranium subcircular in anterior view. Head hairs very few, simple, minute, irregularly scattered. Labrum small and short; posterior surface with spinules of various sizes irregularly arranged and with sensilla of various sizes not clustered near the middle. Mandibles stout and subtriangular; heavily sclerotized; arcuate posteriorly with coarse spinules (not in rows) on the basal half and longitudinal striae on the apical half; apical tooth stout and straight. Galea a truncate cone. Labial palp a low rounded elevation.

Clark, 1925, p. 60: "Although the adult Bull-ant is really a honey-eater, the larvae must have an insect diet or they will eat one another when close together." (Quoted by Wheeler, 1933, p. 22.)

Girault (1915, p. 236) recorded the eucharid *Chalcuroides versicolor* Girault as "parasitic on *Myrmecia* sp." Presumably the larva was parasitoid on the ant larva.

Wheeler, 1910, p. 233: "Smooth, slender larvae, with a rather dense covering of hairs."

Myrmecia gulosa Fabricius.—Plate I, figs. 1-7. Elongate, terete and rather slender. Posterior half definitely the stouter, slightly curved ventrally. Anterior half slender and strongly curved ventrally. Diameter greatest at the fifth and sixth abdominal somites; gradually diminishing forward. Posterior end rounded. Anus subterminal. Leg vestiges moderately large. Segmentation distinct; 10 somites differentiated. Body hairs simple, slightly curved, relatively short (0.06-0.2 mm), uniformly distributed and moderately abundant. Integument spinulose on the ventral surface of pro- and mesothorax. Head very small, subpyriform in anterior view; cranium subcircular, with numerous minute sensilla irregularly scattered over the surface. Head hairs very few, minute (0.03 mm long) and scattered. Antennae mounted on low bulges; small, with three sensilla each. Labrum small and short; breadth twice the length; strongly bilobed due to a wide median incision of the free edge; anterior surface with a few sensilla; posterior surface with several sensilla and

1 Discussion, key and bibliography will follow at the end of Part II.

spinules of various sizes and arranged in various patterns. Mandibles stout, heavily sclerotized throughout, subtriangular in anterior view, arcuate posteriorly; two stout teeth on the medial border and a stout apical tooth; anterior surface with spinules on the basal half and longitudinal striae on the apical half; posterior surface with longitudinal striae on the apical half. Maxillae lobose, round-pointed, with the apical half spinulose; a few hairs (0.04 mm long) on the posterior surface; palp a truncate cone with one apical and two lateral sensilla; galea a truncate cone with a single apical sensillum. Labium subhemispherical; anterior surface spinulose; posterior surface with several hairs (0.04 mm long); palp a low rounded elevation bearing three sensilla; opening of sericteries a conspicuous transverse slit. Hypopharynx coarsely spinulose. (Material studied: several larvae from New South Wales.)

Brues, 1919: Adult eucharids (*Psilogaster fasciiventris* Brues) bred from a cocoon of *M. gulosa*. (Referred to by Wheeler, 1928, p. 42.) Presumably the larvae had been parasitoid on the ant larvae.

Wheeler, G. C., 1938, p. 141: "A larva . . . has short (0.045 mm) transverse lines (slits?)" on the meso- and metathorax. These are provisionally termed "wing rudiments."

Myrmecia sanguinea F. Smith.—Body and head hairs a little longer; maxillary palp and galea longer and slenderer; otherwise very similar to *gulosa*. (Material studied: fragments of three larvae from New South Wales.)

Wheeler, 1918: "It is milk-white, has the form of a vegetable marrow, with all the segments distinct, except those at the extreme posterior end of the body, the anterior segments are very slender and curved and the head is very small. The body is rather uniformly clothed with short, rapidly tapering bristle-like hairs. Under a higher magnification the head is seen to have a projecting bilobed clypeus, broad, heavily chitinized, coarsely tridentate mandibles and well-developed maxillae and labium, the former with two pairs of strongly chitinized peg-shaped sensillae, the latter terminating in a broadly elliptical chitinous plate, with a single pair of knob-shaped sensillae and the opening of the salivary duct near the middle of its anterior border. The upper surface of the short, rounded cranium bears a pair of minute antennal rudiments. . . . It is . . . not improbable that the *Myrmecia* larva is fed on whole insects, since the small head and very long mobile neck are very much as in certain solitary wasp larvae (*e.g., Sphecius*), which gnaw a small hole in their prey and then reach into its body cavity and devour its soft parts. The mandibles of the *Myrmecia* larva certainly show that it feeds on insect food" (pp. 296-298). Fig. 1 on p. 297—photograph of two adult larvae of *Myrmecia sanguinea* in side view. Fig. 2 on p. 298—head in dorsal, ventral and lateral views.

Myrmecia forficata Fabricius.—Forel (1890) found adult eucharids (*Eucharis myrmeciae* Cameron) in the cocoons of this bullfrog ant. (Referred to by Brues, 1919, p. 13 and by Wheeler, 1928, p. 41.)

Myrmecia nigriceps Mayr.—"The larvae were feeding on small clusters of

recently killed Camponotus workers, which had been cut in two at the petiole." (Wheeler, 1933, p. 39.)

Myrmecia regularis Crawley.—Wheeler (1932) uses this species as the paradigm of the intermittently claustral method of colony-feeding. As soon as the first larvae hatch the queen leaves her nest from time to time to capture insects with which to feed them.

Wheeler, 1933: "The slender, small-headed and long-necked larvae are fed on pieces of insects or even on entire or nearly entire insects" (p. 26). "Nearly half-grown larvae . . . were sometimes found feeding on fresh pieces of insects, such as caterpillars and the gasters of deälated ant females" (p. 28). "Young larvae feeding on a piece of caterpillar" (Fig. 6 opposite p. 26).

Myrmecia simillima F. Smith.—Wheeler (1933, p. 34) found "a compact cluster of young larvae which were devouring a fresh saw-fly larva."

Myrmecia (*Promyrmecia*) *mandibularis* F. Smith.—"The larvae are fed on insects. In one nest I found a cluster of them devouring a decapitated cricket." (Wheeler, 1933, p. 67.)

Myrmecia (*Promyrmecia*) *pilosula* F. Smith.—"The larvae are fed on pieces of various insects." (Wheeler, 1933, p. 57.)

Tribe AMBLYOPONINI Forel

Genus MYSTRIUM Roger

Body hairs long, simple and flexuous, with the apical half very slender. Cranium broader than long; narrowed ventrally; occipital border broadly rounded. Head hairs none. Spinules on posterior surface of labrum mostly in short transverse arcuate rows, but those near the ventral border are isolated. Mandibles stout, subtriangular and heavily sclerotized; lateral part thick, medial part blade-like; apical tooth stout and nearly straight. Labial palp a low elliptical elevation.

Mystrium camillae Emery.—Plate I, fig. 19-20. Body hairs abundant, long (0.13 mm), flexuous, apical half very slender, uniformly distributed (except on anterior part of prothorax, which is naked but with spinulose integument). Cranium somewhat broader than long; narrowed ventrally; occipital border broadly rounded. Head hairless but with a few scattered sensilla. Antennae of moderate size; three sensilla each. Labrum a little longer than broad; conspicuously bilobed (because of a deep median notch in the free border); 10 sensilla on the anterior surface near the ventral border; several on the posterior near the midline; posterior surface spinulose, the spinules minute and grouped in short transverse arcuate rows, except those near ventral border which are coarse and isolated. Mandibles stout, heavily sclerotized, subtriangular in anterior view; with two stout teeth on the medial border; apical tooth obtuse and round-pointed; medial portion of apical half thin and blade-like, lateral portion much thickened posteriorly; a few longitudinal striae on the anterior surface of the blade-like portion. Maxillae lobose and round-pointed; palp a short paxilla with one finger-like apical sensillum and three short rounded lateral sensilla; galea finger-like, with an apical sensillum.

Labium spinulose; palp an elliptical elevation bearing four sensilla, one of which is a slender paxilla. Opening of sericteries wide and conspicuous. Hypopharynx densely and coarsely spinulose. (Material studied: a single broken larva from the Philippine Islands.)

Genus STIGMATOMMA Roger

Body hairs short to long, simple, slightly curved. Cranium with angulate lateral borders; upper half semicircular in anterior view. No hairs on head. Labrum small, short and broad; posterior surface spinulose, the spinules near the ventral border isolated, the remainder grouped in short transverse arcuate rows. Mandibles stout and subtriangular; medial border deeply furrowed and trough-like, bearing three teeth; also three teeth on the anterior surface; apical tooth curved medially and posteriorly; anterior surface smooth. Labial palp a low rounded elevation.

Cook (1905, p. 38) says that the larvae of this genus have a uniform coat of fine hairs.

Wheeler, 1903, p. 209: "The larva [of *Cerapachys augustae*] is intermediate between that of Eciton and Stigmatomma. It is covered with shorter, less flexuous, and less abundant hairs than the latter and in these particulars resembles the larvae of Eciton."

Wheeler, 1910, p. 233: "Smooth, slender larvae, with a rather dense covering of hairs."

Stigmatomma pallipes (Haldeman).—Plate I, figs. 8-11 and Text fig. 1. Shaped somewhat like a crookneck squash; thorax and first two or three abdominal somites forming a long slender curved flexible neck; the remainder of the abdomen stout and straight. A welt-like ridge along either side of the abdomen, separating the strongly convex dorsum from the less convex venter and continued forward as a series of bosses on the sides of the neck. Posterior end broadly rounded. Anus ventral. Eleven differentiated somites; segmentation conspicuous in the neck; less so elsewhere. Leg vestiges present. Body hairs abundant and uniformly distributed, simple, slightly curved, 0.05-0.2 mm long. Integument of ventral surface spinulose. Head longer than broad. In anterior view the sides of the cranium are angulate while the upper half is semicircular; without hairs but with a few scattered sensilla. Antennae mounted on the ends of oval elevations; small; with three sensilla each. Labrum small, short and broad; bilobed, the ventral border having a narrow and moderately deep notch; seven sensilla on the ventral border of each lobe; numerous sensilla near center of posterior surface; posterior surface spinulose, the spinules near the ventral border isolated, the remainder grouped in short transverse arcuate rows. Mandibles stout, heavily sclerotized, roughly triangular in anterior view; trough-like, with the medial surface deeply grooved lengthwise; the stout apical tooth strongly curved medially and posteriorly; three teeth on the anterior surface and three on the medial border. Maxillae conoidal, with the apex spinulose; palp a short stout peg with four lateral sensilla and one on the apex; galea curved, finger-like, with a single apical sensillum.

Labium large; anterior surface spinulose, the spinules arranged in short transverse rows; palp a rounded boss bearing five sensilla; opening of sericteries wide and conspicuous. Hypopharynx spinulose. (Material studied: numerour larvae from Connecticut, New Hampshire and New York.)

Escherich, 1906, Fig. 30 = 1917, Fig. 36A = Wheeler, 1900, Fig. 8a.

Text fig. 1.—*Stigmatomma pallipes* (Haldeman). Larvae, ×11

Haskins (1928) gives as the life cycle: egg, 40-60 days; larva, 137-233 days; pupa 41-57 days (p. 182). "Trophallaxis forms the bond between adults and larvae but no larvae has been observed to be fed with liquid food. *Pallipes* has been seen to pinch larvae to assist in the exudation of fluids—no doubt the remnant of a primitive Vespine trick. Larvae quickly devour dead members of the brood, but no larva has been observed to actually kill another, or to devour ova. Young larvae have occasionally been accidentally impaled on the sharp mandibles of adults, indicating a significant lack of care on the part of the nurses in their handling of the young" (p. 183).

Wheeler, 1900: "The body is rather slender in alcoholic specimens, and the segments are all quite distinct and clothed rather uniformly and densely with yellowish hairs, which under a high power are seen to taper into very slender flexuous points. The head is somewhat longer than broad and without hairs on its dorsal surface, the labrum is bilobed, the maxillae provided with the usual tactile cones. The outer one of these on either side appears to be bifurcate. The young differs from the mature larva only in having a relatively larger head and a sparser covering of bristles. . . . The larva of *Stigmatomma* . . . does not conform to the Ponerine type but closely resembles, instead, the larvae of certain Myrmicinae, which are also covered with hairs instead of bristly tubercles. . . . The larvae are fed in the very same manner as other Ponerine larvae. . . . A large larva was seen with its head and neck inserted in the two last segments of a beetle larva." When provided with Formica larvae, the Stigmatomma larvae sucked their juices "till they were reduced to shriveled skins" (pp. 61-62). Fig. 8 on page 61 (repeated 1910 as Fig. 38 on p. 72) shows a larva in side view, the head in anterior view and a hair.

Wheeler, 1903, p. 209: The larvae are characterized as "nontuberculate."

Wheeler and Mann, 1914, p. 10: "The larvae . . . are . . . very broad behind and very narrow and curved anteriorly and instead of being tuberculate, have the body covered with dense, soft, erect hairs."

Genus AMBLYOPONE Erichson

Body hairs simple, slender, flexuous. Anus terminal. Cranium subcircular in anterior view. Head practically naked; hairs very few, simple, exceedingly minute. Labrum very small, subrectangular; not bilobed; posterior surface spinulose, the spinules arranged in short transverse arcuate rows. Mandibles elongate and slender; base feebly sclerotized and only slightly dilated, apex strongly sclerotized; apical tooth slightly curved medially and posteriorly; two stout medial teeth; anterior surface with longitudinal grooves. Labial palp a low elliptical elevation.

Amblyopone australis Erichson.—Plate I, figs. 12-18. Shaped somewhat like a crookneck squash; thorax and first two abdominal somites forming a long slender curved flexible neck. The remainder of the abdomen stout. A welt-like ridge along either side of the abdomen, separating the strongly convex dorsum from the less convex venter, and continued forward as a series of bosses on the sides of the neck. Along each dorsal and ventral margin of ridges and bosses are several curious structures (exudatoria?) of various shapes. Posterior end broadly rounded. Anus terminal. Eleven differentiated somites. Leg vestiges present. Spiracles small. Body hairs moderately numerous, uniformly distributed, flexuous, 0.12-0.2 mm long. Integument spinulose (at least on the ventral surface of prothorax). Head small; cranium subcircular in anterior view. Head hairs very few (about 8) and exceedingly minute (0.009 mm). A few sensilla on the surface of the head. Antennae mounted on slight bulges; small; each with three sensilla. Labrum a moderately thick flap, subrectangular, broader than long; a shallow median notch in the free edge, with a median longitudinal groove on the anterior surface leading upward from the notch; on either side of the notch is a boss bearing three sensilla; anterior surface with numerous sensilla near the free border, posterior with a few sensilla near the base; posterior surface spinulose, the spinules grouped in short transverse arcuate rows. Mandibles long and slender; base feebly sclerotized and only slightly dilated; apical two-thirds subcylindrical and strongly sclerotized; tip curved medially and posteriorly; apex sharp-pointed; anterior surface with longitudinal grooves; with two stout teeth on the medial border near its apical third. Maxillae large, lobose, spinulose; spinules on medial surface coarse; fine spinules in short arcuate rows on the anteroventral surface; palp subcylindrical and moderately long; with two apical sensilla and a lateral finger-like projection bearing an apical sensillum; galea large, finger-like, with two apical sensilla. Labium large, prominent and coarsely spinulose; palp a low elliptical elevation bearing three sensilla, one of which is on the tip of a finger-like projection; opening of sericteries conspicuous. (Material studied: fifteen larvae from New South Wales and Tasmania.)

Wheeler, 1933, p. 75: "The larvae are fed with bisected or entire insects, as the following observations show: . . . devouring an Elaterid beetle nearly an inch long, which the workers had brought in and cut in two at the junction of the prothorax and mesothorax. Two of the larvae had thrust their small, narrow heads and slender necks deeply into the small opening at the anterior end of

the mesothorax in order to reach the soft tissues at the only vulnerable point of the heavily armored prey."

Amblyopone cephalotes F. Smith.—Very similar to *australis*. The mandible as a whole is stouter; its apical tooth is stouter and blunter. (Material studied: 4 larvae from New Zealand.)

Tribe PARAPONERINI Emery

Genus PARAPONERA F. Smith

Neck stout and strongly curved; body stouter, elongate, straight and subcylindrical. Spiracles minute. Body hairs simple and slightly curved; mostly short, a few minute. Midventral surface naked. Head practically naked; with several exceedingly minute simple hairs. Cranium subtrapezoidal in anterior view. Labrum very small; posterior surface spinulose, with the spinules isolated and not arranged in any pattern. Mandibles stout and subtriangular, with the lateral part thick and the medial part blade-like; apical tooth stout and straight; anterior surface with reticulated striae on the base. Maxillary and labial palps each with five apical sensilla, one of which is a paxilla.

Paraponera clavata (Fabricius).—Plate II, figs. 1-9. Thorax and first abdominal somite forming a rather stout but strongly curved neck. The remainder of the abdomen stouter, elongate, straight and subcylindrical. Lateral longitudinal welts broad, low and inconspicuous. Posterior end round-pointed. Anus ventral. Thirteen differentiated somites. Leg vestiges present. Spiracles minute. Body hairs abundant and uniformly distributed, except on the midventral surface, which is naked; simple and slightly curved; short (0.2-0.3 mm); numerous longer (0.4 mm) hairs on the ventral surface and a few scattered elsewhere; a few minute (0.07 mm) hairs irregularly distributed. Integument of ventral surface beset with minute spinules arranged in short arcuate rows. Head small; cranium subtrapezoidal in anterior view, narrower below; with numerous small sensilla and several minute hairs scattered over the surface. Antennae surmounting a low convexity; small; three sensilla each. Labrum small, short and thick; breadth twice the length; free border broadly notched and bearing eight low rounded projections, each with one to three sensilla; anterior surface roughened with irregular bosses and bearing numerous sensilla and several minute hairs; posterior surface spinulose and bearing numerous sensilla; the spinules not arranged in any definite pattern. Mandibles stout and very heavily sclerotized, subtriangular in anterior view; anterior surface of basal half roughened with grooves in an irregularly reticulate pattern; lateral part of distal half thick, curving medially and terminating in a strong blunt apical tooth; medial part blade-like and bearing two stout blunt subapical teeth. Maxillae conoidal; apex densely beset with long slender spinules; palp a subcylindrical peg bearing on its flat apex five sensilla, one of which is peg-like; galea finger-like, with two apical sensilla. Labium large and subhemispherical; applied to the end of an inflated gula; anterior surface densely spinulose; palp a subcylindrical peg bearing five apical sensilla, one of which is peg-like; opening of sericteries wide and salient.

Hypopharynx spinulose. (Material studied: nine larvae from British Guiana.)

Young larva.—Hairs less abundant.

Wheeler (1928) discusses a case of Mermis parasitism in Paraponera and infers that the Mermis larva must enter the ant larva.

Wheeler, G. C., 1938, p. 141: no wing rudiments.

Zahl, 1939: "The larvae are glistening blue-white, helpless creatures capable of very limited movement" (p. 170). Zahl suspects (p. 179) that the larvae (presumably because of exudates) are necessary for or at least highly conducive to the welfare of the captive colony.

Tribe PLATYTHYREINI Emery
Genus PLATYTHYREA Roger

Abdomen with its dorsal profile strongly convex and its ventral nearly straight and serrate; terminal somite forming a stout blunt tail, which is directed ventrally at right angles to the long axis of the abdomen; anus ventral, on the anterior base of the tail; ventral surface of abdomen furnished with seven pairs of tubercles and three transverse ridges. Body and head practically naked, with only a very few scattered minute simple hairs. Cranium subhexagonal. Antennae slender elongate lobose adnate elevations. Labrum small; spinules on posterior surface isolated near the ventral border but elsewhere grouped in short transverse arcuate rows. Mandibles elongate, narrow, heavily sclerotized; base only slightly dilated; arcuate ventrally; apical tooth short, blunt and curved mediaily; medial border serrate with several denticles; anterior surface without spinules.

Wheeler (1910) describes the larvae of this genus as naked on page 73 and on page 233 as "smooth, thickset larvae, with short, sparse hairs and peculiar unpaired tubercles on the midventral surface of some of the abdominal segments."

Platythyrea inermis Forel.—Plate II, figs. 10-18. Thorax and first abdominal somite forming a slender, somewhat curved neck; the remainder of the abdomen stout, with its dorsal profile strongly convex and its ventral profile serrate and nearly straight. Lateral longitudinal welts feebly developed. Diameter greatest at the sixth abdominal somite and diminishing rapidly to the posterior end. Terminal somite forming a sort of stout, blunt tail, which is directed ventrally at right angles to the long axis of the abdomen; anus ventral, on the anterior base of this tail. A pair of tubercles (exudatoria?) on the midventral surface of each abdominal somite, except the first and the last; two transverse ridges on the midventral surface of the seventh abdominal somite and one on the ninth. Twelve differentiated somites. Leg vestiges present. Spiracles small. Body hairs very few, uniformly scattered, simple, minute (about 0.018 mm long). Integument for the most part densely spinulose, the spinules about 0.005 mm long and arranged in transverse rows; those on the mesothorax grading into papillae (0.003 mm) which cover the prothorax and the anterior portions of the mesothorax. Cranium subhexagonal

in anterior view; about as broad as long; occipital border slightly curved. Head naked except for a few sensilla and a very few exceedingly minute (about 0.005 mm long) hairs. Antennae slender elongate lobose adnate elevations narrowed dorsally to a slender ridge which extends obliquely almost to the center of the occipital border; each with three sensilla. Mouth parts large and prominent. Labrum small; breadth at the base one and a half times the length; narrowed ventrally; ventral border with a median lobe and several large sensilla; anterior surface with several sensilia; posterior surface densely spinulose and bearing a few sensilla; spinules on ventral third are isolated but the remainder are grouped in short transverse arcuate rows. Mandibles long, narrow and heavily sclerotized; slightly arcuate posteriorly; not greatly enlarged at the base; with a short blunt apical tooth which is curved medially; distal half of medial border serrate with several denticles. Maxillae paraboloidal; with a patch of spinules at the middle of the anterior surface and another on the apex; palp a rather stout peg with one apical and three lateral sensilla; galea a rather stout finger-like projection bearing a single apical sensillum. Labium large and prominent; anterior surface spinulose; palp a rather stout peg with two apical and three lateral sensilla; opening of sericteries conspicuous. Hypopharynx spinulose. (Material studied: nine larvae from the Philippine Islands.)

Platythyrea meinerti Forel.—Mann (1916, Pl. 7, fig. 53) figures a full-grown larva in side view.

Platythyrea punctata (F. Smith).—Wheeler, 1905, p. 81: "There are no pointed tubercles covering the body as in many other Ponerinae . . . and the hairs are much shorter and sparser. . . . There is a prominent rounded protuberance on the midventral surface of the fifth, and another on the corresponding region of the sixth abdominal segment. The latter protuberance is covered with yellow spinules. The head of the larva is unusually small, with rather feeble mandibles." The figure on page 81 shows the head and the abdomen in ventral view and the entire larva in side view.

Tribe ECTATOMMINI Emery

Wheeler, 1920, p. 48: ". . . the Ectatommiine Ponerinae . . . have elaborate but coarser stridulatory surfaces on the mandibles, so that the larva may be able to produce a variety of sounds and therefore apprise the nurses of more than one need or craving."

Genus PARANAMOPONE Wheeler

Paranamopone relicta Wheeler.—Wheeler, 1915: "The larva is rather slender, pure white and covered with delicate white hairs, which are short and rather dense, especially on the dorsal surface, and interspersed with fewer, longer and more flexuous hairs. The head is rounded, sparsely hairy and bears a pair of well-developed, tridentate mandibles" (p. 119). Wheeler figures a "nearly full grown larva" and the "head of same from above" (Pl. VIII, figs. 7 and 8).

Genus PRIONOPELTA Mayr

Body elongate, terete, moderately slender, slightly curved ventrally. Body hairs simple; grouped in bands around the middle of the somites leaving the intersomitic grooves and adjacent areas conspicuously naked; mostly short, simple and slightly curved, the longer hairs whip-like and restricted to the middle of the somites. Head hairs few, simple, slightly curved, moderately long. Antennae subhemispherical. Labrum short, broad, subrectangular, not bilobed; medial half of posterior surface spinulose, with the spinules in transverse rows. Mandibles elongate and very slender; base only slightly dilated; feebly sclerotized; apical tooth small and slightly curved medially; medial teeth small and acute; anterior surface smooth. Maxillary palp shaped like a bootee; with a spinule-bearing sensillum on the outer edge, a curved finger-like sensillum projecting upward from the "toe" and three spinule-bearing mammillate sensilla decorating the "top." Labial palp a low rounded elevation.

Prionopelta punctulata Mayr.—Plate II, figs. 19-24. Elongate, moderately slender, terete, slightly curved ventrally. Diameter greatest at the fifth abdominal somite; decreasing gradually to the anterior end (*i.e.* no distinct neck) and more abruptly to the posterior end, which is round-pointed. Anus subterminal. Ten differentiated somites. Spiracles minute. Body hairs simple, moderately abundant, grouped in bands around the middle of the somites, leaving the intersomitic grooves and adjacent areas conspicuously naked; length 0.045-0.144 mm; the longer hairs whip-like, restricted to the middle of the somites; shorter hairs slightly curved, not whip-like. Integument with a few spinules on the midventral surface of the thorax. Head large; cranium subcircular in anterior view. Head hairs few, simple, slightly curved, about 0.055 mm long. Antennae small, subhemispherical, each bearing three sensilla. Labrum subrectangular but with the ventral corners rounded and the ventral border feebly concave; short and broad, the breadth twice the length; numerous sensilla on the ventral edge and adjacent part of anterior surface; medial half of posterior surface densely spinulose, with the spinules in transverse rows; a medial cluster of sensilla on the posterior surface near the ventral border. Mandibles feebly sclerotized; elongate and very slender; subcylindrical; base only slightly dilated; apical tooth small, moderately sharp, slightly curved medially; two delicate sharp denticles on the medial border. Maxillae large and lobose; distal surface spinulose; palp shaped like a bootee, with a spinule-bearing sensillum on the outer edge, a curved finger-like sensillum projecting upward from the "toe," and three spinule-bearing mammillate sensilla decorating the "top"; galea a slender finger-like projection with a single apical sensillum. Labium large, protruding, transversely subelliptical; anterior surface spinulose, the spinules arranged in short arcuate rows; palp a low rounded elevation bearing four sensilla, one of which is finger-like; opening of sericteries a wide conspicuous shelf projecting downward. (Material studied: five larvae and two semipupae from Colombia.)

Genus TYPHLOMYRMEX Mayr

Densely and uniformly covered with a mat of branching (mostly trifid) hairs. Head with a few large bifid hairs. Cranium transversely subelliptical. Antennae cylindrical; with three sensilla, each of which bears a long stout spine. Labrum large and thick, subtrapezoidal, with the ventral border feebly incised at the middle; posterior surface spinulose, the spinules minute but becoming longer toward the ventral border and arranged in definite rows which radiate from the dorsolateral angles; rows continuous on basal half of labrum but broken into short components on the ventral half; no spinules near the ventral border. Mandibles with the basal 2/5 greatly inflated and feebly sclerotized; distal 3/5 straight, very slender, strongly sclerotized; apical tooth slender, sharp-pointed, curved medially and posteriorly; medial teeth small and acute; basal half of anterior surface with longitudinal rows of minute spinules.

Typhlomyrmex robustus Emery.—Plate III, fig. 9-12. Shaped somewhat like a crookneck squash; thorax and first two abdominal somites forming a slender neck; remainder of abdomen swollen. Densely and uniformly covered with a mat of branching hairs averaging about 0.1 mm long; hairs typically trifid (rarely bifid or four-branched). Cranium subelliptical in anterior view; short, the breadth 1½ times the length; front bulging. Head hairs few; relatively large; length 0.035-0.07 mm; number and location variable. Each antenna mounted on a small elevation; small, slender, relatively long, subcylindrical; bearing three apical sensilla, each surmounted by a long stout spinule. Labrum large and thick; subtrapezoidal, narrower below; breadth (at base) twice the length; ventral border broadly but feebly incised at the middle; a few sensilla on the anterior surface and six on the ventral border; posterior surface spinulose, the spinules minute but increasing in length toward the ventral border and arranged in definite rows which radiate from the dorsolateral angles, the rows continuous on the basal half but breaking distally into short arcuate components; no spinules near the ventral border; posterior surface with a medial cluster of small sensilla on the lower half. Mandibles large; basal two-fifths greatly inflated and feebly sclerotized, its anterior surface with numerous radiating rows of minute spinules; distal three-fifths straight, very slender, somewhat flattened and strongly sclerotized; apical tooth slender, sharp-pointed, curved medially and posteriorly; two small acute teeth on the medial border. Maxillae paraboloidal; palp a stout peg bearing three apical and one lateral sensilla; galea a slender finger-like projection bearing a single apical sensillum. Labium very large, subhemispherical, applied to the end of a greatly inflated gula; anterior surface spinulose; palp a stout peg bearing several sensilla; opening of sericteries conspicuous. (Material studied: one damaged immature larva and a head; collected by Dr. W. M. Mann in Honduras.)

Genus STICTOPONERA Mayr

Anus terminal. Body with a dense coat of branched (mostly four-branched) hairs, through which project a few longer bifid and simple hairs;

the simple hairs stiff, nearly straight and most abundant at the posterior end. Head hairs few, short, simple, slightly curved. Cranium subhexagonal in anterior view. Antennae minute, paxilliform; with three sensilla, each of which bears a stout moderately long spine. Mouth parts large and conspicuous. Labrum large, subtrapezoidal; ventral border feebly incised at the middle; posterior surface spinulose, the spinules all minute but becoming longer toward the ventral border and arranged in definite rows which radiate from the dorsolateral angles; rows continuous on basal half of labrum but broken into short arcuate components on the ventral half; no spinules near the ventral border. Mandibles large, long and narrow; moderately sclerotized; base slightly dilated; lateral border thickened, medial bladelike; apex slightly curved medially and posteriorly; apical tooth stout, round-pointed; medial teeth small, acute; basal ⅔ of anterior surface beset with numerous spinules arranged in longitudinal rows; spinules mostly minute but along and near the lateral border of the medial half they are exceedingly long.

Stictoponera sp.—Plate III, figs. 1-8. Shaped somewhat like a crookneck squash; thorax and first two abdominal somites forming a slender curved neck; remainder of abdomen swollen and nearly straight. Posterior end round-pointed. Anus terminal. Eleven differentiated somites. Body with a dense coat (about 0.08 mm thick) of many-branched hairs (mostly four-branched), about 0.1 mm long, through which project a few bifid and simple hairs about 0.14 mm long; simple hairs stiff, nearly straight and most abundant at the posterior end. Integumental spinules restricted to the ventral surface of the thorax. Head small and elongate; mouth parts very large and conspicuous; cranium subhexagonal and somewhat broader than long. Head hairs few, short (0.02-0.07 mm), simple, slightly curved; arrangement various and often asymmetrical; only two hairs on clypeus. Antennae minute; each situated on the enlarged end of an elongate rounded ridge; a stout peg, slightly constricted at the base and bearing three apical sensilla, each of which is surmounted by a stout and moderately long spine. Labrum subtrapezoidal, narrowed ventrally; ventral border feebly incised at the middle; numerous sensilla on and near the ventral border; posterior surface with a cluster of minute sensilla near the center; posterior surface spinulose, the spinules all minute but becoming longer toward the ventral border, and arranged in definite rows which radiate from the dorsolateral angles; rows continuous on basal half of labrum but broken into short arcuate components on the ventral half; no spinules near the ventral border. Mandibles large; long and narrow; moderately sclerotized; basal half slightly dilated; apical half rather stout, its lateral border thickened, its medial border blade-like; apex slightly curved medially and posteriorly; apical tooth stout, round-pointed; two small acute subapical teeth on the medial border; basal ⅔ of anterior surface beset with numerous spinules arranged in longitudinal rows; spinules mostly minute but along and near the lateral border of the middle half they are exceedingly long. Maxillae large; apex paraboloidal; anterior surface with minute spinules arranged in short rows; palp a large peg bearing two terminal and two lateral sensilla; galea a large finger-like projection bearing two apical sensilla. Labium large, subhemispherical, applied to the end of a greatly inflated gula; anterior surface thickly beset with coarse

spinules; palp a short stout peg, bearing one lateral and four apical sensilla; opening of sericteries prominent. (Material studied: six larvae labelled "Kalabit Country N. Borneo 3000 ft. E. Mjöberg"; probably a new species.)

Stictoponera sp.—Hairs more abundant and longer; otherwise similar to the larvae from Kalabit. [Material studied: six larvae labelled "Pajan Borneo E. Mjöberg"; probably *S. coxalis* (Roger).]

Genus HOLCOPONERA Mayr

Neck rather stout. Body hairs branched, mostly trifid. Head hairs short, simple or bifid. Antennae minute paraboloidal prominences bearing three sensilla, on each of which is mounted a long stout spine. Mouth parts large and conspicuous. Labrum large; subparabolic in anterior view; ventral border feebly incised at the middle; posterior surface spinulose, the spinules all minute but becoming longer toward the ventral border, and arranged in definite rows which radiate from the dorsolateral angles; rows continuous on the basal half but broken into short arcuate components on the ventral half; no spinules near the ventral border. Mandibles large, moderately sclerotized; dilated at base; apical half slender; apical tooth long, slender, acute, slightly curved medially and posteriorly; medial teeth small and acute; basal ⅔ of anterior surface beset with numerous spinules; spinules on basal third minute, those on the middle third extremely long and slender, giving the rows a comb-like appearance.

Holcoponera striatula Mayr.—Plate III, figs. 13-17. Thorax and first abdominal somite forming a rather stout neck, which is curved ventrally. The remainder of the abdomen stouter, straight and subcylindrical. Lateral longitudinal welts broad, low and inconspicuous. Posterior end rounded. Anus subterminal. Seven or eight differentiated somites. Leg vestiges present. Spiracles minute. Body hairs abundant and uniformly distributed, except for the naked areas adjacent to the intersomitic furrows: dendritic, mostly three-branched, a few bifid, many four- or five-branched; averaging about 0.1 mm long. Head small. Cranium subtrapezoidal (in anterior view) but with the occipital border broadly rounded; much narrowed ventrally. Mouth parts large and prominent. Head hairs few and uniformly distributed; simple or bifid; slightly curved; short (0.027-0.053 mm). Antennae small situated on the ends of elliptical elevations; each a minute paraboloidal protuberance bearing on its apex three sensilla; from each sensillum projects a slender conical spine which is nearly as long as the antenna itself. Labrum a little broader than long; narrowed ventrally; ventral border rounded at the corners and feebly incised at the middle; a few sensilla on the ventral border and adjacent portion of anterior surface; posterior surface with a cluster of sensilla near the center; posterior surface spinulose, the spinules all minute but becoming longer toward the ventral border, and arranged in definite rows which radiate from the dorsolateral angles; rows continuous on basal half but broken into short arcuate components on the ventral half; no spinules near the ventral border. Mandibles rather long and moderately sclerotized; dilated at the base;

apical half slender and bearing two small acute teeth on the medial border; apical tooth long, slender, acute, slightly curved medially and posteriorly; basal two-thirds of anterior surface beset with numerous spinules arranged in longitudinal rows; the spinules on the basal third minute, those on the middle third extremely long and slender and giving the rows a comb-like appearance. Maxillae paraboloidal; apical half spinulose; palp a slender cone bearing one apical and two lateral sensilla; galea only slightly longer than palp, finger-like and bearing a single sensillum on the apex. Labium large and inflated; subhemispherical; anterior surface beset with coarse spinules arranged in transverse arcuate rows; palp a subconical paxilla bearing one apical and two lateral sensilla; opening of sericteries wide and conspicuous. (Material studied: five larvae from Costa Rica.)

Holcoponera brasiliensis Emery.—Similar to *striatula*. (Material studied: three larvae from Brazil.)

Holcoponera rustica wheeleri Santschi.—Similar to *striatula*. (Material studied: eight larvae from Costa Rica.)

Holcoponera striatula angustipleura Forel.—Eidmann, 1936, p. 33: "Die Larven sind schwach gekrümmt und ringsum dicht behaart."

Holcoponera strigata (Norton).—Wheeler, 1903, p. 209: "These larvae are nontuberculate . . . but covered with long, multifurcate, somewhat flexuous hairs."

Genus CHALCOPONERA Emery

Body hairs short; of five types (including simple and branched). Head hairs few, short, simple, slightly curved. Cranium subhexagonal in anterior view. Antennae minute, peg-like; each bearing on its apex three long stout spines. Mouth parts large. Labrum large, subrectangular, bilobed; posterior surface spinulose, the spinule minute but becoming longer toward the ventral border, and arranged in definite rows which radiate from the dorsolateral angles; rows continuous on the basal half but broken into short arcuate components on the ventral half. Mandibles rather stout, subtriangular in anterior view; moderately sclerotized; basal half greatly inflated; apical half thin and narrow, bearing two rather stout medial teeth and terminating in a long slender apical tooth which is curved medially and posteriorly; most of anterior surface beset with minute spinules arranged in longitudinal rows; no combs.

Chalcoponera impressa (Mayr).—Plate IV, figs. 1-8. Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a slender curved neck; remainder of abdomen stout and straight; posterior end rounded. Anus subterminal. Spiracles minute. Body hairs short, moderately abundant, uniformly distributed; of five sorts—(a) short (0.16 mm) rather stout, with the tips frayed; (b) bifid, with simple branches, about 0.26 mm long; (c) unbranched and whip-like, with short stout base and long tenuous lash, about 0.45 mm long; (d) bifid with short stiff base and very long flexuous branches, about 0.45 mm long; (e) trifid but otherwise like (d). Head small with large and prominent mouth parts; cranium subhexagonal in anterior view,

bulging at the middle of each side, the occipital border somewhat rounded. Head hairs few, simple, slightly curved, shorter than body hairs but quite varied in length (0.04-0.12 mm), uniformly scattered. Antennae minute pegs mounted on rounded eminences; each bearing three apical sensilla; each sensillum bearing a long stout spine. Labrum rather large; subrectangular, breadth one and a half times the width; ventral border rounded at the corners, incised at the middle and furnished with numerous large sensilla; posterior surface spinulose, the spinules minute but becoming longer toward the ventral border, and arranged in definite rows which radiate from the dorsolateral angles; rows continuous on basal half but broken into short arcuate components on the ventral half; a cluster of small sensilla on the posterior surface near the center. Mandibles rather stout, subtriangular in anterior view; moderately sclerotized; basal half greatly inflated; apical half thin and narrow, bearing two rather stout medial teeth and terminating in a long slender apical tooth which is curved medially and posteriorly; most of anterior surface beset with minute spinules arranged in rows which radiate from the middle of the dorsal border. Maxillae with the anterior surface sparsely spinulose; palp an elongate cone bearing one lateral and two apical sensilla; galea a finger-like projection bearing a single apical sensillum. Labium very large; anterior surface densely spinulose, the spinules arranged in transverse rows; palp a short stout peg bearing one apical and four lateral sensilla; opening of sericteries wide and conspicuous. Hypopharynx spinulose. (Material studied: three larvae from Queensland.)

Chalcoponera metallica (F. Smith).—Similar to *impressa*. (Material studied: three larvae from Queensland.)

Chalcoponera metallica cristulata Forel.—Brues (1934, p. 204) has described the adult of *Tricoryna chalcoponerae* collected with this ant in New South Wales. From what is known of the life histories of other eucharids, one may infer that the wasp larvae are parasitoids in the ant larvae.

Genus RHYTIDOPONERA Mayr

Body hairs of three types: (a) simple and slightly curved, (b) simple and flagelliform, but mostly (c) bifid. Head hairs several, short, simple, slightly curved. Cranium subelliptical in anterior view. Antennae minute, paraboloidal; each with three moderately long spines on the apex. Labrum bilobed; posterior surface spinulose, the spinules minute but becoming longer toward the ventral border; spinules arranged in definite rows which radiate from the dorsolateral angles; rows continuous on the basal half of the labrum but broken into short arcuate components on the ventral half; on and near the ventral border the spinules are isolated. Mandibles feebly sclerotized; basal half greatly inflated; distal half narrow, of two parts—(1) a large thin obtuse medial tooth and (2) an elongate slender lateral part which terminates in a long slender apical tooth and which has an elongate acute tooth adnate to its medial face; most of anterior surface spinulose, the spinules minute and arranged in longitudinal rows; no combs.

Rhytidoponera cristata Mayr.—Plate III, figs. 19-22. Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a long slender curved neck; remainder of abdomen stout and nearly straight. A welt-like ridge along either side of the abdomen, separating the strongly convex dorsum from the less convex venter. Along the dorsal and ventral margins of the welts are several curious structures (exudatoria?) of various shapes. Posteriorly end broadly rounded. Anus terminal. Leg vestiges elliptical, rather large. Nine differentiated somites. Body hairs moderately abundant and uniformly distributed; of three types—(a) bifid, 0.2-0.3 mm long, the most abundant type, (b) simple, flagelliform, base short and moderately stout, flagellum extremely long and fine, total length about 0.5 mm, limited to the ventral surface, and (c) simple, rather stout, slightly curved, 0.25-0.35 mm long, near the posterior end. Integument spinulose; the spinules exceedingly minute and arranged in transverse rows. Cranium subelliptical in anterior view; slightly broader than long. Head hairs few, irregularly scattered, simple, slightly curved, shorter than body hairs but quite varied in length (0.06-0.19 mm). Antennae minute paraboloidal projection mounted on slight rounded elevations; each bearing three apical sensilla, each of which is surmounted by a stout spinule. Labrum as broad as long, bilobed due to a wide deep median incision of the ventral border; numerous large sensilla on the ventral border and on the anterior surface near that border; numerous smaller sensilla on the posterior surface near the center and near the ventral border; posterior surface spinulose, the spinules minute but becoming longer toward the ventral border; spinules arranged in definite rows which radiate from the dorsolateral angles; rows continuous on the basal half of the labrum but broken into short arcuate components on the ventral half; on and near the ventral border the spinules are isolated. Mandibles feebly sclerotized; basal half greatly inflated; distal half narrow, of two parts—(1) a large thin obtuse medial tooth and (2) an elongate slender lateral part which terminates in a long slender straight round-pointed apical tooth and which has an elongate acute tooth adnate to its medial face; anterior surface of mandibles spinulose, the spinules minute and arranged in longitudinal rows. Maxillae spinulose, the spinules minute, some finer and grouped in short rows, others coarser and isolated; palp a stout truncate cone with five sensilla, four of which bear each a slender paxilla; galea a longer slenderer truncate cone with two apical sensilla, each bearing a slender paxilla. Labium large and protruding; anterior surface densely spinulose, the spinules mostly coarse and isolated; palp a short cylindrical projection, with four sensilla each bearing a slender paxilla; opening of sericteries wide and conspicuous. Hypopharynx spinulose. the spinules slender and grouped in arcuate rows. (Material studied: three larvae from New South Wales.)

Wheeler and Bailey (1920) published a photomicrograph (Pl. III, fig. 19) of the mouthparts of this larva and the following comment (p. 269): "The trophorhinium may be discerned as an arcuate system of extremely fine, parallel ridges extending across the space between the bases of the mandibles. It will be noticed also that the upper surfaces of the latter are very finely and

regularly imbricated. . . . When the mandibles are opened or closed, their imbricated surfaces would naturally rub against the dorsal plate of the trophorhinium, and in forms with large mandibles, like *Rhytidoponera* the latter must overlap more or less when opening and closing and thus also rub against one another. Not improbably, therefore, the rough surfaces of the mandibles may reinforce the triturating and sifting functions of the trophorhinium."

Rhytidoponera convexa Mayr.—Apical tooth of mandibles slightly curved medially, slenderer and noticeably shorter. Otherwise similar to *cristata*. (Material studied: two larvae from Queensland.)

Rhytidoponera froggatti Forel—Plate III, fig. 18. Apical tooth of mandibles is strongly curved medially and all teeth are sharper; galea slenderer. Otherwise similar to *cristata*. (Material studied: two larvae from the Solomon Islands.)

Genus EMERYELLA Forel

Body hairs of four types (a) mostly short, stout, slightly curved or sinuous with several minute lateral branches; (b) a few short trifid, with the branches fine and flexuous; (c) a few bifid, longer, with the branches long, fine and flexuous; (d) a few simple, stout and longer. Head hairs few, simple, slightly curved, fine, short. Cranium subhexagonal in anterior view. Mouth parts large and prominent. Antennae minute, cylindrical, bearing three stout moderately long spinules on the distal end. Labrum large, strongly narrowed ventrally, bilobed; posterior surface spinulose, the spinules minute but becoming longer toward the ventral border; spinules arranged in definite rows which radiate from the dorsolateral angles; rows continuous on the basal half of the labrum but broken into short arcuate components on the ventral half; on and near the ventral border the spinules are isolated. Mandibles large, elongate and rather narrow; basal half moderately dilated; apical half, slender, its lateral border thickened, its medial border blade-like; apical tooth curved medially, round-pointed; proximal tooth on medial border obtuse, distal round-pointed; basal ⅔ of anterior surface beset with numerous spinules arranged in longitudinal rows; most spinules very minute but along and near the lateral border of the middle third a few isolated spinules are exceedingly long.

Emeryella schmitti Forel.—Plate IV, figs. 9-14. Shaped somewhat like a crookneck squash; thorax and first two abdominal somites forming a slender curved neck; remainder of abdomen straight and swollen. Posterior end rounded. Body hairs moderately abundant and uniformly distributed; of four types—(a) about 0.17 mm long, numerous, stout, slightly curved, with several short acute lateral branches, (b) a few trifid, about 0.17 mm long, with the branches fine and flexuous, (c) a few bifid, about 0.23 mm long, with long fine flexuous branches, and (d) a few simple, stout, about 0.25 mm long. Cranium subhexagonal in anterior view; breadth one and one-half times the length; mouth parts large and conspicuous. Head hairs few, scat-

tered, simple, slightly curved, fine and short (about 0.05 mm long). Antennae minute, each a short cylinder bearing three stout apical spinules. Labrum large; wider (at base) than long; narrowed ventrally; ventral border narrowly incised at the middle; numerous sensilla on the ventral border and on both surfaces near that border; posterior surface spinulose, the spinules minute but becoming longer toward the ventral border; spinules arranged in definite rows which radiate from the dorsolateral angles; rows continuous on basal half of labrum but broken into short arcuate components on the ventral half; on and near the ventral border the spinules are isolated. Mandibles large, elongate and rather narrow; moderately sclerotized; basal half moderately dilated; apical half slender, its lateral border thickened, its medial border blade-like; two subapical teeth on the medial border, the proximal blunt-pointed and the distal round-pointed; apical tooth curved medially, round-pointed; basal two-thirds of anterior surface beset with numerous spinules arranged in longitudinal rows; spinules mostly very minute but along and near the lateral border of the middle third a few isolated spinules are exceedingly long. Maxillae with the anterior surface sparsely spinulose; palp a short subconical projection bearing three sensilla—apical, subapical and lateral; galea a finger-like projection bearing two apical sensilla. Labium with the anteroventral surface densely spinulose; palp a short subconical projection bearing five sensilla—one apical, two subapical, one lateral and one basal; opening of sericteries wide and conspicuous. Hypopharynx densely spinulose. (Material studied: a single larvae from Haiti; only the head is in good condition.)

Wheeler and Mann, 1914, p. 10: "The larvae . . . are peculiar, . . . resembling the larvae of *Stigmatomma pallipes* . . . in being very broad behind and very narrow and curved anteriorly and instead of being tuberculate, have the body covered with dense, soft, erect hairs." Fig. 3 (p. 10) shows the larva in side view.

Genus ECTATOMMA F. Smith

Cook, 1905, p. 38: "The larvae, like those of *Stigmatomma*, have a uniform coat of fine hairs."

Girault (1915, p. 228) states that *Tricoryna ectatommae* Girault was "taken from nest of ant, Ectatomma." Presumably the eucharid larva was parasitoid on the ant larva.

Wheeler, 1904, p. 767: "The larva of *Ectatomma* is much more primitive in its characters than that of many other Ponerinae, whereas the larva of *Odontomachus* is much like that of the typical genus *Ponera*."

Wheeler, 1910, p. 233: "Smooth, slender larvae, with a rather dense covering of hairs."

Subgenus ECTATOMMA F. Smith

Swollen posterior part of abdomen elongate and subellipsoidal. Neck short, body hairs long and whip-like, the basal 3/5 stiff and bearing numerous denticles along its sides, the distal 2/5 finely attenuate and lash-like. Head

hairs few, moderately long, rather stout, slightly curved, roughened with several minute denticles along the sides. Cranium suboctagonal in anterior view. Mouth parts moderately large. Antennae small; each a truncate cone bearing on its apex three stout spinules, two short and one long. Labrum large, subrectangular, feebly incised at the middle of the ventral border; posterior surface spinulose, the spinules minute but increasing in length toward the ventral border and arranged in definite rows which radiate from the dorsolateral angles, the rows continuous on the basal 2/3 but broken distally into short arcuate components; isolated spinules on and near the ventral border. Mandibles large and rather stout; base broad and feebly sclerotized; apex narrow and strongly sclerotized; apical tooth long and slender, curved medially and posteriorly; subapical teeth acute, the distal much the larger. Most of the anterior surface beset with spinules arranged in longitudinal rows. Maxillae with the lateral surface concave.

Ectatomma tuberculatum (Olivier).—Plate IV, figs. 15-26. Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a short slender curved neck (longer and more slender in younger larvae); rest of abdomen elongate swollen, straight, subellipsoidal. Posterior end rounded. Anus subterminal. Leg vestiges present. Ten differentiated somites. Body hairs abundant and long (0.3 to 0.5 mm); arranged around the somites in distinct bands which are separated by naked intersomitic zones; whip-like, the basal 3/5 stiff and bearing numerous denticles along its sides, the distal 2/5 finely attenuate and flexuous. Integument spinulose; spinules exceedingly minute (about 0.0018 mm); a few in rather regular transverse rows, but mostly arranged irregularly. Cranium suboctagonal in anterior view but with corners broadly rounded. Mouth parts moderately large. Head hairs few, moderately long (0.10-0.15 mm), rather stout, slightly curved, roughened with several minute denticles along the sides. Antennae minute; mounted on low rounded elevations; each antenna a low truncate cone with three apical sensilla; two sensilla bear each a short stout spine, the third a stout curved spine twice as long. Labrum large, subrectangular, a fourth broader than long; moderately incised at the middle of the ventral border; a few sensilla on and near the ventral border; posterior surface with a cluster of minute sensilla near the middle; posterior surface spinulose, the spinules minute but increasing in length toward the ventral border and arranged in definite rows which radiate from the dorsolateral angles, the rows continuous on the basal 2/3 but broken distally into short arcuate components; isolated spinules on and near the ventral border. Mandibles large and rather stout; subtriangular in anterior view; base broad and feebly sclerotized; apex narrow and strongly sclerotized; apical tooth long and slender, curved medially and posteriorly; two acute subapical teeth on the medial border, the distal much larger than the proximal; most of anterior surface beset with spinules arranged in longitudinal rows. Maxillae with the apex conoidal and spinulose, the spinules minute and arranged in short longitudinal rows; lateral surface concave; palp a stout peg with four sensilla (one apical, one subapical, two lateral); galea

a stout finger-shaped projection bearing two apical sensilla. Labium subhemispherical, applied to the end of an inflated gula; anterior surface thickly beset with coarse spinules, those near the midline grouped in short arcuate rows, those at the sides isolated; palp a short peg with four sensilla. Hypopharynx densely furnished with both fine and coarse spinules. (Material studied: numerous larvae from Costa Rica and Panama.)

Text fig. 2—*Ectatomma* (*Gnamptogenys*) *tortuolosum* (F. Smith). A larva infested with two phorid maggots, ×9.

Cook, 1905: "It does not appear that the keleps have the art of regurgitating food for their larvae or for each other, but they have, instead, the curious habit of opening their mandibles wide and lapping up drops of nectar, moistened sugar, or honey on their mouth parts. The liquid is thus carried into the nest and dispensed to the other members of the community, old and young" (p. 17). "Workers occasionally lay eggs" which are "at once fed to the larvae" (p. 18). "Two larvae of unusual size were raised, one of which emerged as a normal winged queen. . . . The time required for the development of a queen is about three months, the larval and pupal stages being about one and one-half times as long as those of the workers" (p. 22). "The extent to which the keleps normally depend upon nectar has not been adequately learned as yet. It may be that they use it largely, if not exclusively, for feeding the very young larvae, since these do not seem to be regularly fed with animal food, captured insects always being given, as far as observed, to the large larvae. Colonies fed exclusively on sugar or honey have raised larvae to nearly the full size, but these seldom, if ever, pupate normally, and in some of the captive colonies very few pupae have survived to emerge as adults" (p. 42). The workers construct over the larvae which are ready to pupate "a cell of earth, if no other materials are at hand, but prefer pieces of old cocoons if these are obtainable" (p. 43). "The brood cells of the kelep are built over the larva as it lies on the floor" (p. 44). "The kelep larvae are not so completely helpless as those of bees and true ants, being provided with mouth parts adapted for eating out the soft interior tissues of insects, and long, flexible necks to enable them to reach inside and clean out the sections of boll weevils laid by the workers carefully on the fat stomachs of their baby sisters. Two such, lying side by side, each provided with a weevil's front leg to nibble, was the ludicrous sight observed in the nest of one of the captive colonies in Texas. Mrs. Cook has noted another instance of feeding which well illustrates the extent to which the social organization has developed in this respect. A worker seized a termite as soon as it was dropped into the nest and held it in its jaws for fully five minutes, the termite vigorously protesting with its anten-

nae. After it was dead, or at least motionless, the kelep took it below where other workers assisted in feeding it to a large larva. It was very hard to get the termite properly placed; time and again it fell from where it had been put, and was turned over and twisted in all sorts of ways in the effort to bring it into a position so that the larva might take hold of its head. The larva meanwhile moved its own head back and forth, evidently trying to get hold on its own account, and a little larva nearby did secure a hold on the other end of the termite, so that the keleps had to move both larva and termite in their further efforts to give the latter to the large larva. The little larva was almost as large as the termite. Finally the matter was arranged, the termite lying across the two larvae, which remained peacefully side by side, the big one eating at the head, the little one at the tail. A worker had to take the head of the big larva between his jaws and fore legs and put it in contact with the termite, and then stood over it as though to see that the larva did its duty. The weight of the small larva kept pulling the termite off the body of the large larva before it had become firmly attached, so a worker stayed by and kept pulling the termite back in position. Finally the large larva got to work in earnest, and the faithful nurse left to help another kelep with another termite" (p. 46).

Weber (1946, p. 5) refers to Cook's account as follows: "The slender larvae 'have long flexible necks which enable them to reach inside and clean out the sections of boll weevils laid by the workers carefully on the fat stomachs of their baby sisters.' The workers covered the larvae with dirt when the latter were ready to pupate, pupation in colonies introduced into Texas taking one and one-half hours."

Cook also reported (p. 15) the emergence of a few specimens of *Isomerala coronata* Westwood from captive colonies. (Referred to by Wheeler, 1907, p. 17.) Presumably the eucharid larvae were parasitoid on the ant larvae. In this connection it is interesting to note that a larva of *tuberculatum* collected in Panama (Changuinola District, August 3, 1924, G. C. Wheeler, No. 169) has a planidium attached to the ventral surface at the junction of head and prothorax. The anterior end of the planidium is directed toward the posterior end of the host. The planidium is 0.1 mm long (exclusive of caudal spines), while the ant larva is about 5 mm long. The attachment to the host was so secure that it resisted boiling in potassium hydroxide solution.

Wheeler (1928a, p. 166; 1928b, p. 205; 1930) discussed mermithegates of this ant and inferred that the nematode larvae (Mermis) had been parasitic in the ant larvae.

Ectatomma quadridens (Fabricius).—Similar to *tuberculatum*. (Material studied: three larvae from Brazil.)

Mann, 1916, Fig. 54 on Pl. 7: larva in profile. (Copied by Gallardo, 1918, Fig. 6 on p. 35.)

Ectatomma ruidum Roger.—Similar to *tuberculatum*. (Material studied: four larvae from Panama Canal Zone.)

Weber, 1946, p. 12: The larvae in an observation nest "rasped the integument of the callow of everything removable. The lower mouth parts were used with the aid of the sharp mandibles above. One larva pierced a femur and, when fluid exuded, the clear liquid was drawn into the mouth, presumably by capillarity. . . . Two other larvae were feeding steadily on a termite, one larva being on its side, the other resting on its dorsal surface. . . . Larvae had also apparently been feeding on sugar. . . . The long hairs of the larvae were clearly of service in keeping them off the wet floor. The larvae were seen to progress slowly forward by an undulating motion and could also raise the anterior half of the body in the air at times. . . . Three larvae had their heads inside the carcass of a fly given them the previous day." Larva in profile, Fig. 3 on p. 15.

Ectatomma edentatum Roger.—Emery (1901, p. 431) describes a larva about 6 mm long:—"È una larva di tipo ponerino, con i quattro primi segmenti dopo il capo sottili, costituenti un collo, al quale segue il resto del corpo rigonfiato che costituisce un addome voluminoso. Tutta la superficie del corpo e ricoperta di numerosi peli semplici, assottigliati all'estremità, come quelli della larva di *Dorylus;* questi peli sono di lunghezza ineguale, ma tutti della medesima struttura. Nessun vestigio di tubercoli o punte o spine. Il colore della larva conservata nello spirito è bigio brunastro, come sono al solito le larve mature di Ponerine prima di avere filato il bozzolo. Il capo della larva è poco meno lungo del segmento seguente dal quale è separato per mezzo di una strozzatura pronunziata che accenna ad una notevole mobilità. Le parti boccali sono robuste. Il labbro superiore bruno è inciso nel mezzo, con due paia di papille e altrettanti brevi peli conici, vicino all'incisura. Le mandibole molto scure sono forti e tridentate. Le mascelle e il labbro inferiore sono come nelle altre ponerine. Sul capo, si vedono molti peli semplici e un paio di minute papille sormontate ciascuna da due minuti peli. Io ritengo che siano rudimenti di antenne. (Pl. II: fig. 10, larva in side view; fig. 11, head in side view; fig. 12, head in anterior view; fig. 13, mandible; fig. 14, antenna.)

Subgenus PONERACANTHA Emery

Swollen posterior part of abdomen subovoidal. Neck long. Prothorax nearly naked. Body hairs rather short, varying in shape between two extremes: at one extreme—slender, slightly curved, with several small slender acute lateral branches; at the other—stout, somewhat flattened, with numerous longer branches, which are occasionally bifid. Head hairs few, simple, minute. Antennae, a pair of minute truncate cones, each bearing three short stout apical spines. Labrum large; slightly broader at the base than long; ventral corners strongly rounded; a conspicuous incision at the middle of the ventral border; posterior surface spinulose, the spinules minute but increasing in length toward the ventral border and arranged in definite rows which radiate from the dorsolateral angles, the rows continuous on the basal two-thirds but broken into short arcuate components on the distal third. Mandibles large, elongate, rather narrow; basal half moderately dilated; distal half with its lateral border

thickened and its medial border blade-like; apical tooth long, slender, round-pointed; medial teeth small and acute; basal three-fourths of anterior surface beset with numerous spinules arranged in longitudinal rows; spinules mostly minute but along and near the lateral border a few isolated spinules are exceedingly long. Labial spinules coarse and isolated.

Ectatomma (*Poneracantha*) *bispinosum* Emery.—Plate V. figs. 1-5. Shaped somewhat like a crookneck squash; thorax and first two abdominal somites forming a long slender curved neck; remainder of abdomen swollen and subovoidal. Posterior end rounded. Anus subterminal. Leg vestiges present. Body hairs moderately abundant and uniformly distributed (except for the prothorax which is nearly naked); short (length 0.21-0.25 mm); varying in shape between two extremes; at one extreme—slender, slightly curved, with several small slender acute lateral branches; at the other— stout, somewhat flattened, with numerous longer branches, which are occasionally bifid. Integument spinulose, the spinules minute and arranged in transverse rows. Head pear-shaped; cranium as broad as long; mouth parts moderately large. Head hairs few, scattered, simple, minute (0.023 mm). Antennae minute; each mounted on the ventral end of an elongate low narrow rounded ridge; each a rather stout truncate cone bearing three short stout apical spines. Labrum large; slightly broader (at base) than long; ventral corners broadly rounded; a conspicuous incision at the middle of the ventral border; several sensilla on and near the ventral border; a cluster of small sensilla near the center of the posterior surface; posterior surface spinulose, the spinules all minute but increasing in length toward the ventral border and arranged in definite rows which radiate from the dorsolateral angles, the rows continuous on the basal two thirds but broken into short arcuate components on the distal third. Mandibles large, elongate and rather narrow; moderately sclerotized; basal half moderately dilated; distal half with its lateral border thickened and its medial border thin and blade-like; apical tooth long, slender, round-pointed, curved medially and posteriorly; two small acute subapical teeth on the medial border; basal three fourths of anterior surface beset with numerous spinules arranged in longitudinal rows; spinules mostly minute but along and near the lateral border a few isolated spinules are exceedingly long. Maxillae spinulose; palp peg-like, with four or five sensilla; galea finger-like, with one or two apical sensilla. Labium with the anterior surface densely spinulose, the spinules long, coarse, sharp and isolated; palp a short peg with four or five sensilla; opening of sericteries conspicuous. Hypopharynx beset with slender delicate spinules arranged in short arcuate rows. (Material studied: four larvae from Panama.)

Subgenus PARECTATOMMA Emery

Plate V, figs. 13-16. Resembles Poneracantha except in the following characters:— Body hairs of two main types: (1) sinuate, with three to eight minute acuminate lateral branches, 0.18-0.21 mm long; (2) furcate, about 0.16 mm long, with two to four (mostly four) long branches; there are also

intergrades between these types. Antennae slender elongate cylinders, each bearing three short stout spines on the distal end. Labial spinules fine and grouped in short arcuate rows. (Material studied: eight larvae of *E.* (*P.*) sp. from Barro Colorado Island, Panama Canal Zone; collected by G. C. Wheeler, July 21, 1924, No. 254.)

Subgenus GNAMPTOGENYS Roger

Plate V, figs. 6-12. Resembles Poneracantha except in the following characters:—Neck short; swollen posterior part of abdomen subellipsoidal and straight (as in the subgenus Ectatomma). Body hairs of four types (with intergrades): (1) simple, nearly straight, about 0.16 mm long; (2) sinuate, about 0.18 mm long, with a few minute acuminate lateral branches; (3) straight or slightly curved, 0.14-0.17 mm long, with longer slender lateral branches; (4) bifurcate, 0.1-0.28 mm long, the most abundant type. Prothorax with numerous hairs. Head small. Labrum with the sides more nearly parallel; median incision in ventral border slightly deeper. Mandibles with the apical tooth slenderer and more curved; medial teeth slightly larger. (Material studied: numerous larvae of *E.* (*Gn.*) *tortuolosum* (F. Smith) and one of *E.* (*Gn.*) *mordax* (F. Smith) from British Guiana.)

The larvae of *tortuolosum* are labelled "Kartabo, B. G. VII-14-1920 No. 69" and were evidently collected by Dr. W. M. Wheeler. They are particularly interesting because eight out of fifteen larvae contain parasitoid maggots. Six contain one maggot each and two contain two maggots each (Text fig. 2). The spiracles of the maggots are applied to breathing holes made through the integument of the host. Apparently these holes may be located on any part of the ant larva except the head and first two thoracic somites. One of these holes (in a cleaned and stained integument) is elliptical and measures 0.035 x 0.070 mm; its rim is raised, rounded, heavily sclerotized and 0.026-0.053 mm wide. Four additional ant larvae have one or two such holes through the integument but contain no evident parasitoids. Five semipupae removed from cocoons show no evidence of infestation. Mr. Willis W. Wirth of the United States National Museum has kindly examined the maggots and written as follows: "These appear to me to belong to the family Phoridae, but possess several modifications for parasitic habit which makes this determination less sure. There are two small elevations at the posterior end which correspond well in shape and position to those on which the posterior spiracles are usually borne in Phoridae. But in these larvae the spiracles seem to have migrated along a very slender sclerite alongside the large ventral anal plate, to occupy a position about halfway up on the abdomen. In the un-dissected ant larva, these spiracles can plainly be seen to protrude outside the body of the ant."

Tribe PROCERATIINI Emery
Genus PROCERATIUM Roger

Short and stout; with a stout curved neck and a short round-pointed tail, which are both bent ventrally so that head and tail are pointed toward each

other; remainder of body stout and subcylindrical. Body surface thickly beset with large hemispheroidal bosses. Head and body practically naked; hairs very few, widely scattered and exceedingly minute. Head moderately large; its surface roughened with several low bosses which in turn have their surfaces tuberculate. Antennae large, not projecting. Mouth parts very large. Labrum considerably broader than long, narrowed at the base; lateral borders sinuate; ventral border slightly concave; not spinulose. Mandibles small and feebly sclerotized; acuminate; no medial teeth; no spinules. Maxillae very large; with only a few minute spinules; palp represented by a few scattered sensilla. Labium large; with only a few minute spinules; opening of sericteries consisting of a pair of truncate cones separated by an angular projection.

Proceratium croceum (Roger).—Plate V, figs. 20-27. Short and stout; thorax and first abdominal somite forming a very stout neck which is bent ventrally at right angles to the main axis and then posteriorly; terminal somite forming a small ellipsoidal tail which is pointed downward and forward at an angle of about 45° to the main axis; remainder of abdomen subcylindrical. Anus at base of tail on ventral side. Body surface thickly beset with large hemispheroidal bosses, which are arranged for the most part in longitudinal rows. Segmentation indistinct. Body practically naked; body hairs simple, very few, exceedingly minute (0.009 mm long); occurring only on bosses; not more than three to a boss. Dorsal and ventral bosses at anterior end have the integument roughened by coarse spinules which are not arranged in any distinct pattern; the three posterior dorsal bosses, however, have fine spinules arranged in short arcuate rows; intermediate bosses have intergrading spinules; lateral bosses and the integument between bosses lack spinules. Head moderately large; mouth parts very large; cranium subpentagonal in anterior view; middle of posterior border subangulate; surface roughened with several low bosses, each of which in turn has its surface roughened with several small tubercles. Head practically naked; a very few, simple, exceedingly minute (about 0.007 mm long), widely scattered hairs. Antennae a pair of large low rounded elevations, each with three sensilla. Labrum a thick flap; breadth 1½ times the length; narrowed at the base, widest near the ventral border, which is slightly concave; lateral borders sinuate; several sensilla on both surfaces near the ventral border; no spinules. Mandibles small and feebly sclerotized; subtriangular in anterior view; narrow, acuminate, sharp-pointed; no medial teeth; no spinulose surfaces. Maxillae very large and lobose; medial face with a small patch of minute spinules; palp represented by a few scattered sensilla; galea a finger-shaped projection with two apical sensilla. Labium large; a small patch of minute spinules near the center of the anterior surface; palp a low elevation bearing three sensilla; opening of sericteries wide and salient, consisting of two divergent truncate cones separated by a median angular projection. (Material studied: a single damaged specimen from Virginia.)

Young Larva.—Length 0.7 mm. Plump; strongly curved ventrally, so that the mouth and anus are closely approximated; dorsal profile very long

and C-shaped; ventral very short; ventral surface of abdomen broad, convex and protruding at the center; body very broad due to a distinct flange on either side extending from the first through the eighth abdominal somites; each flange is about one eighth of the total width. Terminal somite forming a broad rounded tail, which is pointed forward. Body naked. Integument thickly beset with minute spinules, except on the lateral flanges, which are smooth. Head naked and smooth; cranium subhexagonal in anterior view. (Material studied: several specimens from Mississippi.)

Half-grown Larva.—Length 1.25 mm. Plump; still curved ventrally but with the middle of the body somewhat straightened; ends farther apart but still pointed toward each other; lateral flanges deeper, narrower and broken into incipient bosses by intersomitic furrows; bosses have developed on the thorax and on the ventral surface of the abdomen. Body naked. Integument densely spinulose except on the sides. Head naked; rudiments of a few bosses have appeared. (Material studied: a single specimen from Virginia.)

The following notes are based upon observations made in an artificial formicary in this laboratory in July, 1931; the living larvae and workers of *P. croceum* were collected in Mississippi and sent to us through the courtesy of Dr. M. R. Smith: The larvae (all immature) were sluggish but moved actively upon tactile stimulation. When disturbed the head and tail were repeatedly approximated and separated. The broad and somewhat flattened ventral surface served as a table for food. The tail aided in holding the food. When a larva was offered the viscera of a mealworm, they were seized by approximation of head and tail. The mouth parts were applied to the food; bubbles passed into the body rhythmically at intervals as short as two seconds. The mandibles moved but served no apparent function. The larvae were translucent—almost transparent—and colorless except for many small white lumps beneath the integument; these might have been clumps of urate crystals.

Several of the living larvae referred to above were infested with tarsonemid mites, which were identified by Dr. H. E. Ewing of the United State National Museum as *Pigmephorus* sp.

Haskins, 1930, pp. 123-124: "The larvae, when hatched, are left on the egg packet for three or four days, and during this period are not differentiated by the nurses from unhatched ova. The larvae are short and thick set, with large heads, and are noticeably inactive. They show no tendency to devour unhatched eggs, and during the first week of life give no indication of hunger, nor are they, as far as could be observed, fed. When about a week old, the larvae are removed from the unhatched eggs, and are then placed on whatever food may chance to have been brought into the brood chamber. Even at this stage they show none of the activity usual to Ponerine larvae, but attach themselves to their victims and remain in this position for days, feeding extremely slowly. While feeding they are eagerly licked for exudates, and some indication has been seen of a tendency to pinch them to hasten the flow. When full-fed they drop from their victims, more after the fashion of the larvae of

solitary wasps than of ants, and are then allowed to lie singly on the chamber floor. Growth, under artificial conditions at least, is extremely slow. The larvae have never been seen to move, their complete immobility reminding one strongly of the behavior of many Myrmicine larvae, and contrasting strangely with their thoroughly entomophagous habits. No verifiable case has been seen by the writer in which any attempt was made by a nurse to feed the larvae by regurgitation, although the mouth and the first thoracic segments of the larvae were often assiduously licked, perhaps to obtain a minute quantity of saliva present with the exudates.

"When disturbed, the brood nurses eagerly seize both eggs and larvae and hurry away with them. When undisturbed, however, they showed an increasing tendency to neglect the larvae more and more as the latter grew older, and in every case the young when two or three months old were no longer placed on the insect material brought into the nest to be devoured by the adults. The young made no attempt to help themselves, but shriveled and soon perished, when they were either thrown away or devoured by the nurses."

Proceratium crassicorne Emery.—Plate V, figs. 17-19. The profile of this larva seems at first glance to be quite different from that of *croceum*, but we suspect that the difference is artificial, *i.e.*, the result of preservation, and that the profile of *croceum* is the more natural.

The larvae of the two species are essentially alike, but since the specimen of *crassicorne* is in better condition than that of *croceum*, we append a few details better shown in the former: The bosses range in diameter from 0.04 to 0.17 mm in diameter; those on the dorsal surface are transversely elongate (*i.e.*, subelliptical in dorsal outline); no bosses along the middorsal line. On the ventral side the prothorax forms one large boss; the midventral surface of abdominal somites II-VII is raised into rounded transverse ridges which are subelliptical in ventral outline. The bosses are distributed as follows: prothorax, 13; mesothorax, 12; metathorax, 12; abdomen I, 12; II, 14; III, 16; IV, 12; V, 12; VI, 12; VII, 8; VIII, 4; IX, 2; X, 2. Integument of dorsal and ventral bosses spinulose; dorsal bosses with coarse isolated scattered spinules about 0.007 mm long, which grade posteriorly into short arcuate rows (up to 0.0018 mm long) of finer and shorter (about 0.002 mm long) spinules on the last three somites; ventral bosses with coarse isolated scattered spinules; lateral bosses practically smooth; integument adjacent to bosses with short arcuate rows of spinules (except on abdominal somites IV, V and VI, where such spinules are lacking). (Material studied: a single specimen from Alabama.) (To be concluded)

EXPLANATION OF PLATES

PLATE I. *Myrmecia gulosa* Fabricius, Figs. 1-7.—1, larva in side view, x2.8; 2, two body hairs, ×115; 3, right mandible in anterior view, ×67; 4, head and thoracic segments showing leg and wing vestiges in ventral view (hairs omitted), ×7; 5, mesothoracic legs in ventral view, ×44; 6, head in anterior view, ×33; 7, labrum in posterior view, ×74.

Stigmatomma pallipes (Haldeman), Figs. 8-11.—8, head in anterior view, ×95; 9, two body hairs, ×185; 10, larva in side view, ×21; 11, left mandible in anterior view, ×185.

Amblyopone australis Erichson, Figs. 12-18.—12, right mandible in anterior view, ×93; 13, larva in side view, ×10; 14, head in anterior view, ×56; 15, body hair, ×113; 16-18, three structures found on the borders of the welt, ×90.

Mystrium camillae Emery, Figs. 19-20.—19, left mandible in anterior view, ×117; 20, left mandible in posterior view (shaded to show thickness), ×117.

PLATE II. *Paraponera clavata* Fabricius, Figs. 1-9.—1, head in anterior view, ×25; 2, labrum in posterior view, ×57; 3, larva in side view, ×3; 4, left maxilla in anterior view, ×57; 5, palp of left maxilla in anterior view, ×185; 6, right mandible in anterior view, ×57; 7, right mandible in posterior view (shaded to show thickness), ×57; 8, spinules on ventral surfaces of prothorax, ×235; 9, body hair, ×45.

Plathythyrea inermis Forel, Figs. 10-18.—10, larva in side view, ×17; 11, body hair, ×133; 12, midventral surface of abdomen, ×17; 13, right antenna in anterior view, ×117; 14, papillae on prothorax in profile, ×433; 15, spinules on abdominal integument in profile, ×433; 16, head in anterior view, ×95; 17, spinules on hypopharynx in anterior view, ×433; 18, right mandible in anterior view, ×148.

Prionopelta punctulata Mayr, Figs. 19-24.—19, head in anterior view, ×111; 20, right mandible in anterior view, ×191; 21, left maxillary palp in anterior view, ×470; 22, left antenna in side view, ×236; 23, larva in side view, ×25; 24, two body hairs, ×236.

PLATE III. *Typhlomyrmex robustus* Emery, Figs. 9-12.—9. head in anterior view, ×95; 10, right mandible in anterior view, ×235; 11, head in side view, ×95; 12, body hair, ×185.

Stictoponera sp. [from Kalabit], Figs. 1-8.—1, head in anterior view, ×95; 2, antenna and base in anterior view, ×593; 3, 4, 6, 8, four body hairs, ×212; 5, larva in side view, ×12; 7, left mandible in anterior view, ×185.

Holcoponera striatula Mayr, Figs. 13-17.—13, head in anterior view, ×97; 14, left mandible in anterior view, ×167; 15, left antenna in anterior view, ×697; 16, two body hairs, ×167; 17, outline of body in side view (hairs omitted), ×12.

Rhyidoponera froggatti Forel, Fig. 18.—Outline of body in side view (hairs omitted), ×6.

Rhytidoponera cristata Mayr, Figs. 19-22.—19, three body hairs, ×44; 20, left antenna in anterior view, ×340; 21, right mandible in anterior view, ×95; 22, head in anterior view, ×39.

PLATE IV *Chalcoponera impressa* (Mayr), Figs. 1-8.—1, left antenna and base in anterior view, ×185; 2, right mandible in anterior view, ×100; 3, head in anterior view, ×57; 4-8, five body hairs, ×57.

Emeryella schmitti Forel, Figs. 9-14.—9, head in anterior view, ×57; 10, 11, 13, 14, four body hairs, ×72; 12, left mandible in anterior view, ×72.

Ectatomma (*E.*) *tuberculatum* (Olivier), Figs. 15-26.—15, right antenna and base in anterior view, ×210; 16, head in anterior view, ×55; 17, body hair, ×107; 18, larva in side view, ×8; 19, head in posterior view showing attached planidium, ×55; 20, labrum in posterior view (right half only), ×95; 21, spinules of integument arranged in irregular pattern, ×185; 22, spinules of integument arranged in short rows, ×185; 23, labrum and hypopharynx in anterior view (left half only), ×95; 24, left mandible in anterior view, ×82; 25, left maxilla in anterior view, ×95; 26, midventral surface of meso- and metathorax showing leg vestiges and alveoli of hairs, ×44.

PLATE V. *Ectatomma* (*Poneracantha*) *bispinosum* Emery, Figs. 1-5.—1, head in anterior view, ×55; 2, right antenna in anterior view, ×235; 3, right mandible in anterior view, ×95; 4-5, two body hairs, ×95.

Ectatomma (*Parectatomma*) sp., Figs. 13-16.—13, right antenna in anterior view, ×235; 14, profile of larva, ×6; 15-16, two body hairs, ×95.

Ectatomma (*Gnamptogenys*) *tortuolosum* (F. Smith), Figs. 6-12.—6-7 and 9-12, six body hairs, ×95; 8, profile of larva, ×6.

Proceratium crassicorne Emery, Figs. 17-19.—17, abdominal segment II in dorsal view, ×23; 18, abdominal segment IV to end of body in ventral view, ×23; 19, larva in side view, ×23.

Proceratium croceum (Roger), Figs. 20-27.—20, head in anterior view, ×59; 21, a dorsal boss in side view, ×167; 22, right mandible in anterior view, ×89; 3, body hair, ×370; 24, very young larva in ventral view, ×23; 25, very young larva in side view, ×23; 26, half grown larva in side view, ×23; 27, mature larva in side view, ×23.

PLATE I

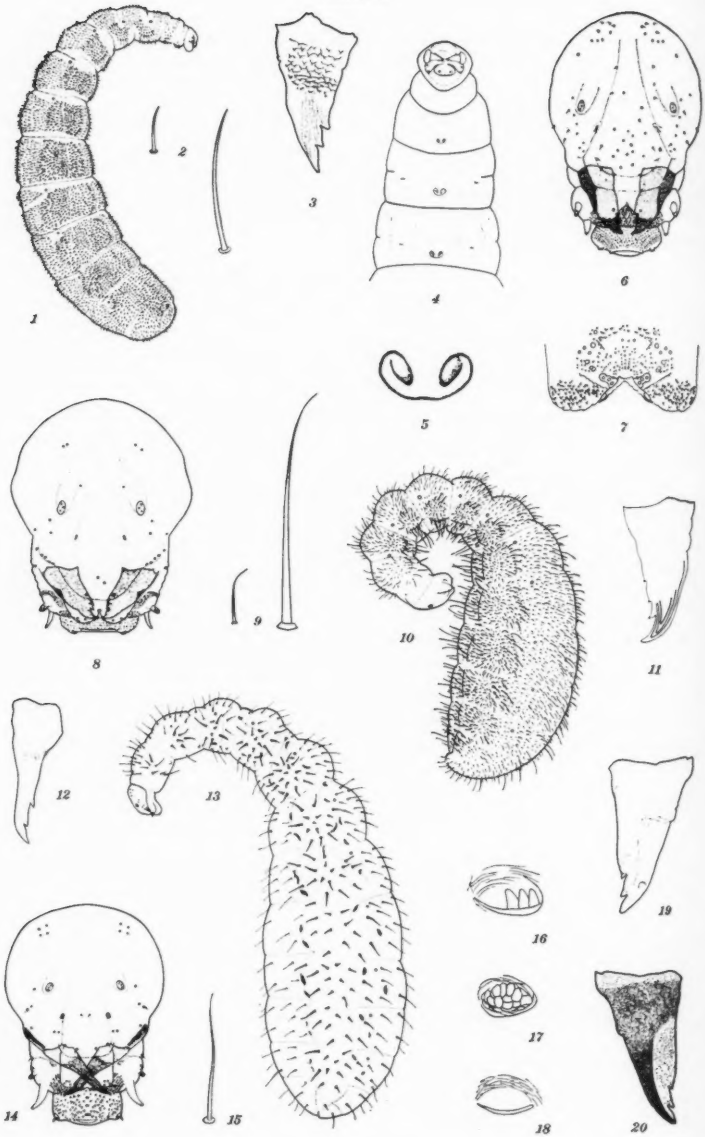


PLATE II

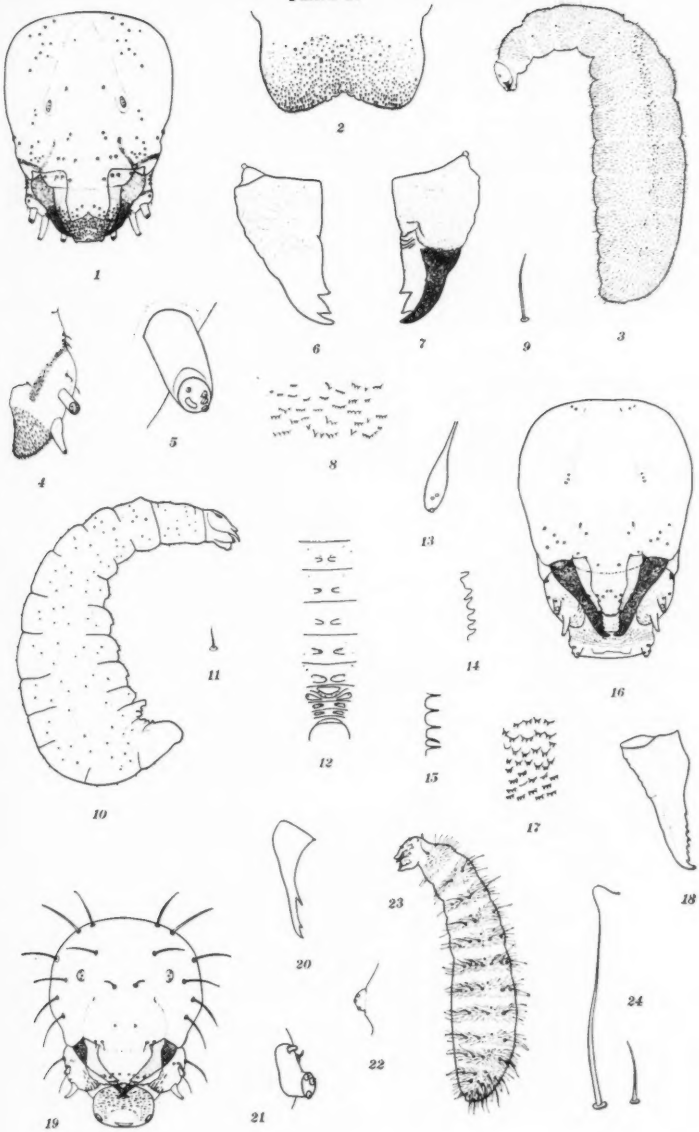


PLATE III

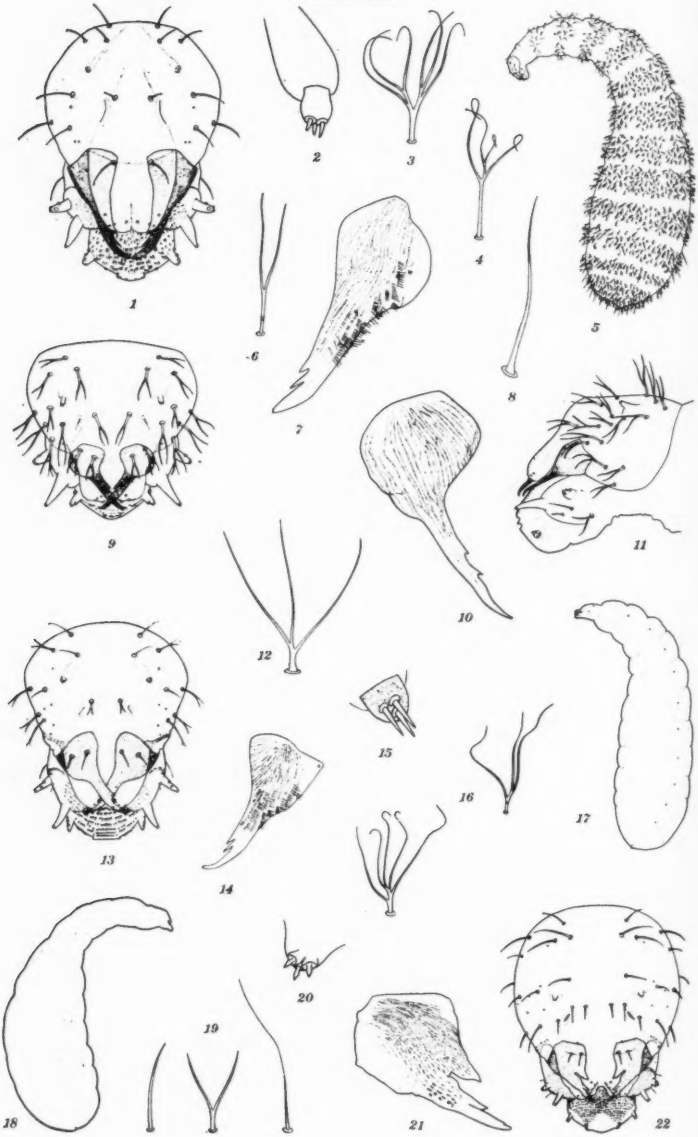


PLATE IV

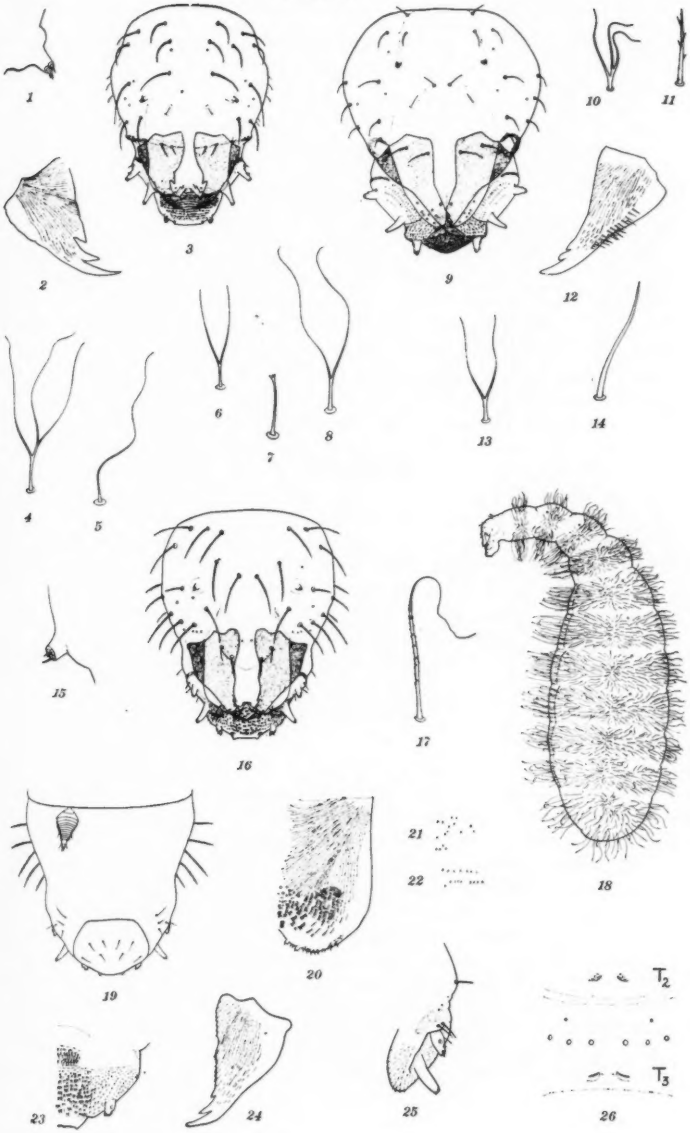
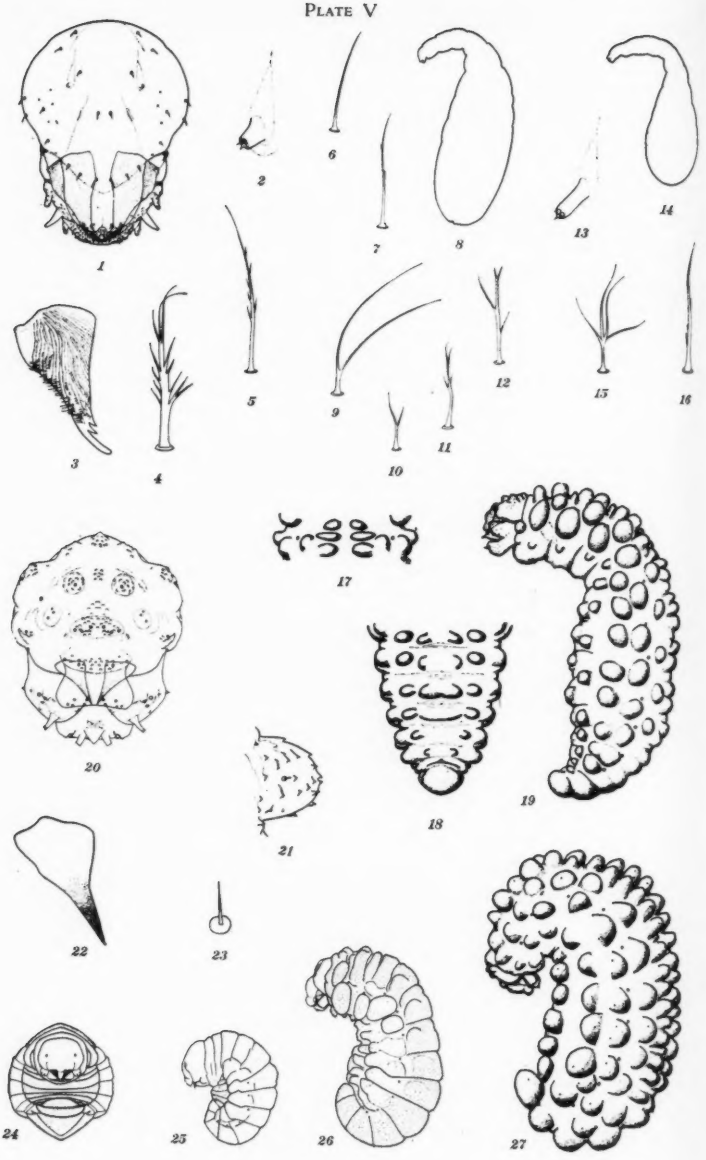


PLATE V



Additional New Species in the Genera Anopompilinus, Anoplius, Pompilinus, and Pycnopompilus (Hymenoptera: Psammocharidae) and Corrections of Previous Papers

R. R. Dreisbach
Midland, Michigan

Five new species of the genus *Pompilinus* and one each in the genera *Anopompilinus* and *Pycnopompilus* and two in the genus *Anoplius* have been found in several lots of spider-wasps which have been received for study since the three papers (Dreisbach, 1949a, 1949b, 1950) on these genera were written. The descriptions of these species follow.

In the paper on the Genus *Pompilinus* (Dreisbach 1949a) the photomicrographs of the male genitalia of *P. texanus* were omitted and the genitalia listed, as this species was a second photo of *P. rectangularis* Dreisbach. The photo of the last ventrite as given there is correct. The photo of *P. texanus* Dreis. is given in the plates as fig. 13. In the paper on *Anopompilinus* (*Dreisbach,* 1949b) the photomicrograph of the genitalia of *A. parvulus* Banks was very poor and there was no photo of the last ventrite. A better specimen of the genitalia is shown in fig. 11, and a photo of the last ventrite is shown in fig. 12. In the paper on *Pycnopompilus* (Dreisbach, 1950) there was no photo of the last ventrite of *P. eureka* (Banks) and that is shown in fig. 21. Also the fig. 41 in the 1950 paper was the last ventrite of *P. scelestus* (not that of *P. lasiope* as named). Fig. 20 shows the last ventrite of *P. lasiope*. In the 1949b reference the names for the cubital and sub-discoidal veins were interchanged in the figures.

Pompilinus utahensis n. sp.
Figs. 15,16.

Holotype male—Completely black, with clypeus, face, inner orbits to just above antennae, front of basal antennal joint, and posterior orbits on apical half with finely appressed silvery pubescence; thorax with very short white hair over most of the surface but not with the silvery sheen of clypeus except at the outer apical corners of propodeum, just below tegulae, and on fore coxae; the finely appressed hair of abdomen blackish; numerous long hairs on vertex, front, under clypeus, under head, fore coxae, and on pronotum; when seen from the side, the clypeus has a slight bulge, the whole front is above eyes, with the greatest height at the antennal fossae, the nearer ocellus is visible above the eyes, and the eyes are much broader than the posterior orbits; when seen from in front, the vertex is level with the eyes, the ocellar triangle is slightly raised above the surface, there is a slight emargination about the middle of the eyes, with the eyes slightly closer together at the clypeus than at the emargination; ocelli in a high triangle,

with the fore ocellus twice its diameter from the laterals and these as far apart as their distance to eyes; no sulcus or line in front of anterior ocellus; ratio of lengths of the first four and last two antennal joints are as 25:10:20:25:15:20; apex of clypeus appearing slightly curved due to the convex dorsal surface; mandibles reddish at the apical third; pronotum angulate on posterior margin, and flat on the dorsal surface; propodeum in a smooth curve from base to apex; abdomen without any upright hair except a very few apically; wings smoky throughout, no more so at tip than the rest of wing; the two recurrent veins meet the second and third cubital cells at apical third and much beyond the middle respectively; second cubital cell about one third as long on marginal vein as on cubitus, third cubital cell strongly petiolate; marginal cell very small, less than one half as long as its distance to wing tip; median vein in fore wings slightly basad of the transverse median, and the subdiscoidal vein in rear wings slightly basad of the cubitus; femora devoid of spines except posterior pair have a few small ones; fore tibiae with a few small spines on the ventral surface and at tip, the last two pair have a few spines on dorsal surface and on the sides; last two pair of legs have a few spines on the metatarsal joints and a few on the second tarsal joint but the rest of the joints almost devoid of spines except at the tip; all the claws cleft or split, but the inner ray much shorter than the outer, more so than in most of the species of the genus; longer spur of posterior tibiae two-thirds as long as its metatarsal joint; comparative lengths of joints of posterior legs, femora through tarsi 25:25:17.9:6:4:8.

Length: Head and thorax 3.02 mm, abdomen 2.4 mm, fore wing 4.64 mm, rear wing 3.76 mm, genitalia length 1.06 mm, width 0.53 mm, last ventrite length 0.73 mm width 0.53 mm.

Holotype male: Castle Dale, Utah, VI-24-41, G. F. Knowlton. (U.S.N.M.)

It is necessary to have the last ventrite to identify this species. The parameres approach those of *P. incitus* Evans, slightly, but are broader, the parapenial lobes are longer than the aedeagus, which flares out at tip as is usual in the genus. The last ventrite is very much like that of *P. stenotus* (Banks), except that it has only very tiny hairs on the sides beyond the edge of the midrib, and it has a row of about five hairs on outer basal third, and the volsellae are of a different shape at the tip.

Pompilinus submarginatus n. sp.

Figs. 14, 17.

Holotype male.—Completely black except the apical third of the mandibles are reddish; face, clypeus, inner orbits to above antennae, and posterior orbits on the lower half, with finely appressed white sericeous pubescence; the coxae and part of thorax also slightly sericeous; when seen from the side, the clypeus has only a very slight bulge, all the front above the eye level in increasing amount from the fore ocellus to antennal fossae, the nearer lateral ocellus is completely visible, eyes are very broad, the posterior orbits are very narrow, only about three eighths as broad as the eyes; when seen from in front, the vertex is at the same level as the eyes and almost

flat except for a slight bulge at the ocellar triangle, a slight emargination on inner orbits about the middle, lower part of eyes almost parallel; fore ocellus twice its diameter from the laterals and these as far apart as their distance to eye margin; a very few long hairs on vertex, under clypeus, under head, on neck, and pronotum; fore ocellus in a slight pit and an indication of a sulcus running forward; ratio of first four and last two antennal joints are as 25:10:20:22:15:20; pronotum only very slightly angulate on posterior margin; propodeum with hardly level dorsal surface, in a smooth curve from base to tip, with no upright hair; wings smoky, with beautiful greenish, iridescent reflection; second cubital cell about one-half as long on marginal vein as on cubitus, third cubital cell petiolate; marginal cell small, much shorter than its distance to wing tip; the two recurrent veins meeting the second and third cubital cells at the apical third and much beyond the middle, respectively; basal and transverse veins in fore wings interstitial, and the subdiscoidal vein in rear wings basad of the cubitus; a few spines on last two pair of femora; the legs spined just about like those of utahensis above; claws all split or cleft; longer spur of posterior tibiae two-thirds as long as their metatarsal joints; ratio of lengths of joints of posterior legs femora through tarsi are as 25:24:18:8:4:3:5.

Length: Head and thorax 2.65 mm, abdomen 3.0 mm, fore wing 4.3 mm, rear wing 3.6 mm, genitalia length 0.79 mm, width 0.59 mm, last ventrite length 1.13 mm, width 0.39 mm.

Holotype male: Delta, Utah, VI-25-49, G. F. Knowlton. (U.S.N.M.)

This species belongs in the marginatus complex, where it is necessary to have the last ventrite and the genitalia to distinguish the species.

The genitalia is very much like that of *P. marginatus*, except that the parameres are not quite so wide and the parapenal lobes are longer than the aedeagus, while in marginatus they are of the same length. However, the last ventrite is entirely different as it is acute at tip, and expands in width gradually, while in marginatus the tip is obtuse and is as wide just back of the tip as it is at middle. This ventrite has just about the same shape as *P. truncatus* Dreisbach.

Pompilinus minutus n. sp.

Figs. 7, 8.

Holotype male.—Completely black, with the apical third of mandibles reddish; the only sericeous hair is on the apical, outer corners of the propodeum and on the coxae; long hair on head, vertex, under head, fore coxae; with a very few short hairs on apical edge of last tergite and last ventrite and on pronotum; when seen from the side, the clypeus is without a bulge, only the fore half of front visible above the eyes, ocelli and vertex not visible, and posterior orbits about three-fourths as wide as eyes; when seen from in front, the vertex is slightly arched, with the ocellar triangle slightly above the surface, only a slight indication of an emargination on inner orbits, and the eyes approach each other at the clypeus; ocelli in a rather high triangle, the fore ocellus about twice its diameter from the laterals,

and these as far apart as their distance to eyes; no sulcus in front of anterior ocellus; ratio of lengths of first four and last two joints of antennae as 20:8:18:18:16:16; pronotum slightly angulate on posterior margin, thorax covered with small, appressed, light brown hair; hardly any of propodeum in a horizontal plane but arches in a smooth curve from base to apex; wings brown; marginal cell very small, only five-twelfths as long as its distance to wing tip; the two recurrent veins meet the second and third cubital cells beyond apical third and about the middle respectively; second cubital cell small, third very slightly petiolate; basal vein in fore wings basad of the transverse vein and the subdiscoidal in rear wings is much basad of the cubitus; legs spined just about as in the preceding species, except that there are fewer spines on the tibiae; fore claws split, the rest missing; the longer spur of posterior tibiae two-thirds as long as its metatarsal joint.

Length: Head and thorax 2.65 mm, abdomen about 3.3 mm, fore wing 4.0 mm, rear wing 3.3 mm, genitalia length 0.73 mm, width 0.53 mm, last ventrite length 0.99 mm, width 0.53 mm.

Holotype male: Tancitaro, Michoacan, Mexico, 6600′, VII-2-5—1940, Hoogstraal and Knight. (MCZ)

Paratype male: Length head and thorax 2.2 mm, abdomen 3.3 mm, fore wing 3.5 mm, rear wing 3.0 mm, genitalia length 0.73 mm, width 0.53 mm, last ventrite length 0.86 mm, width 0.59 mm.

Paratype: Oaxaco, Oaxaco, Mexico, semi-desert, 5000′, VII-20-1937. Collection of G. E. Bohart.

This is a very small species, with one exception the smallest of the genus. The genitalia and last ventrite are very much like those of *P. estellina* Banks, but the parameres are much narrower. The length of the male of estellina was given by Banks as 8.0 mm, whereas this species is only 5.3 mm long, yet the genitalia is almost as long and is much wider than that species, while the last ventrite has the length and width in a much different ratio, as in this species it is shorter than in the other but is wider. The last ventrite does not have the row of hairs at the outer edge near the base, but it does have two very tiny ones.

Pompilinus shappirioi n. sp.

Figs. 5, 6.

Holotype male.—Completely black with the apical third of mandibles reddish; face and front a short distance above antennae, with silvery pubescence, clypeus shows only a trace but it seems to be covered over, and should also show it in other specimens; all the coxae completely covered, except the base, with very dense, silvery pubescence which has a golden tinge, the edge and apex of propodeum also covered with silvery pubescence, but not as dense as in the case of coxae; all the thorax slightly sericeous, the abdomen not glistening but covered with very small, finely appressed, whitish hair; when seen from the side, the clypeus has only a very slight bulge and is almost straight from the base to tip, front extending above the eyes in a smooth curve from fore ocellus to antennal fossae with the highest point about midway in the curve, eyes broad, about three times as wide as the

posterior orbits; when seen from in front, the vertex is straight across, but with a slight bulge at the ocellar triangle, a slight emargination of the eyes at the highest part of front, the eyes approach each other slightly at the clypeus; fore ocellus about its diameter from the laterals, and these about one and one-third as far apart as their distance to eye margin; ratio of lengths of the first four and last two antennal joints as 25:10:21:24:16:24; pronotum almost transverse on posterior margin, just bare indication of angulation; a long dorsal almost horizontal portion to the propodeum, this part partly inclined, but with a rather abrupt angle near the apex; wings slightly smoky, much more so beyond the cells; marginal cell small, only about three-fifths as long as its distance to wing tip; second cubital cell almost as high as broad, slightly shorter on marginal vein than on cubitus, third cubital cell petiolate, longer on the cubitus than the second cell; the two recurrent veins meet the second and third cubital cells at the middle and beyond the middle respectively; basal vein in fore wings basad of the transverse, and the subdiscoidal vein in rear wings basad of the cubitus; legs spined similarly to the species above; claws all clefs; longer spur of posterior tibiae three-fourths as long as its metatarsal joint; ratio of lengths of the joints of rear legs femora through tarsi as 105:105:80:40:30:17:30.

Length: Head and thorax 2.65 mm, abdomen 2.7 mm, fore wing 4.0 mm, rear wing 2.6 mm, genitalia length 0.79 mm, width 0.46 mm, last ventrite length 0.92 mm, width 0.52 mm.

Holotype male: Washington, D. C., VII-10-48, David Shappirio (MCZ).

Through the courtesy of Mr. Shappirio this type will be deposited in the collection of The Museum of Comparative Zoology at Harvard University.

This is another species in the marginatus complex, but is distinct from any other species of the genus by virtue of the row of long hairs on the inner edge of the parameres. The parameres are not as broad as those of marginatum, the volsellae are not as broad as in *marginatus* and they are as long as the parameres and the parapenial lobes, whereas in *marginatus* they are shorter, and further the volsellae are more pointed. The last ventrite has somewhat the same general shape as in *marginatus*, but has a pointed, acute tip, and it is more than half as wide as long, while in *marginatus* it is only one-third as wide as long, and further the opaque midrib has no long hair and it is wedge shaped, and the sides have no long hair at all, while *marginatus* is well haired on the sides.

Pompilinus basirufus n. sp.

Figs. 9, 10.

Holotype male.—Black, the tip of mandibles slightly reddish, and the first two abdominal segments are completely red as well as the third tergite; the clypeus, face, and front to slightly above antennae, very strongly sericeous, with rather long appressed hair, the coxae and trochanters very strongly sericeous on the ventral surfaces, with the under side of femora, sides of pronotum, plate under tegulae, and outer apical corners of propodeum with much less sericeous hair; the red parts of abdomen with a slight bloom, the

black part slightly shining, with a small red spot in middle of the fourth tergite, while the base of first tergite is black; when seen from the side, the clypeus has no bulge whatever, but is straight from the antennae to tip of clypeus, about one-half of front just back of antennae visible above the eye, vertex not visible but the nearer, lateral ocellus is completely visible, posterior orbits only one-fourth as wide as eyes; anterior ocellus its diameter from the laterals and these not quite twice as far apart as their distance to eye margin; a slight sulcus in front of fore ocellus; ratio of lengths of the first four and last two antennal joints are as 30:10:30:30:20:30; a few long hairs on vertex, under clypeus, and shorter ones on pronotum, with none on the propodeum; pronotum very slightly angulate on posterior margin, a long inclined dorsal surface on propodeum; wings very smoky, with brilliant, greenish, iridescent reflection; marginal cell two-thirds as long as its distance to wing tip; both recurrent veins received by their respective cubital cells much beyond the middle; second cubital cell slightly more than one-half as long on the marginal vein as on the cubitus, third cubital cell petiolate and as long on cubitus as the second cubital; basal vein of fore wing basad of the transverse vein and the cubitus apicad of the subdiscoidal in rear wings; longer spur of posterior tibiae nine-tenths as long as its metatarsal joint; ratio of lengths of the joints of posterior legs femora through tarsi are as 29:30:22:10:7:5:8.

Length: Head and thorax 3.3 mm, abdomen approx. 4.3 mm, fore wing 5.4 mm, rear wing 4.7 mm, genitalia length 0.93 mm, width 0.54 mm, last ventrite length 1.26 mm, width 0.53 mm.

Holotype male: Gainesville, Fla., V-1-49. From collection of David Shappirio. Will be deposited in Museum of Comparative Zoology at Harvard College.

Paratype: Horry Co., S. C., Myrtle Beach, VIII-29-49, IX-6-49, David Shappirio. (RRD) Length: head and thorax 3.7 mm, abdomen 4.3 mm, fore wing 6.0 mm, rear wing 4.6 mm.

This is another species in the marginatus group. The genitalia is very much like that of marginatus, but the parapenial lobes are longer than the aedeagus or volsellae and the volsellae are very slightly longer than the aedeagus, while in *marginatus* the parapenial lobes are not quite as long as aedeagus and the volsellae are shorter than parapenial lobes and aedeagus; the last ventrite, however, is entirely different as is shown by the figure. The genitalia and last ventrite are almost exactly like those of *P. submarginatus* n. sp. above, but that species is entirely black, while this species has almost half of the basal part of abdomen red, and further the longer spur of posterior tibiae is nine-tenths of the length of its metatarsal joint in this species while in the species named it is only two-thirds as long, and also the comparative lengths of the joints of the posterior pair of legs are entirely different as can be seen from the measurements given above. Both species have the beautiful greenish, iridescent reflection in the wings.

Allotype female.—Black, with the dorsal surface and sides of tergites one and two, and the dorsal, basal half of tergite three red, the mandibles with the apical half also slightly reddish; a few scattered, long, upright hairs on vertex, front, clypeus, mandibles, anterior edge of fore coxae, pronotum, on

ventral surface of abdomen and on last tergite, the hairs on ventral surface scattered mostly on the apical three-fourths, while the ones on last tergite are long and rather stiff, reminiscent of the genus *Anoplius;* very few appressed hairs on any part of body, but some very fine ones on dorsal surface and sides of propodeum, coxae and abdomen, which are slightly glistening in reflected light; the whole body somewhat shining; when seen from the side, the clypeus is without a bulge and straight to the apical fourth where it bends down slightly, no part of vertex or front visible above the eyes, eyes broad, at least five times as wide as posterior orbits, which are very narrow; when seen from in front, the clypeus is arched from side to side, is truncate at tip with a narrow smooth edge, vertex level with eyes but ocellar triangle just visible above the surface; anterior ocellus slightly larger than the laterals and slightly more than its diameter from them, and these three fourths as far from the eye margin as they are apart; a prominent line from the anterior ocellus to antennae; ratio of lengths of the first four and last two antennal joints are as 9:3:15:13:6:6; pronotum slightly angulate on posterior margin; propodeum slightly declivous; fore wings almost black, darker beyond cells and rear wings very dusky, both with beautiful, brilliant, greenish iridescent color in reflected light; third cubital cell strongly petiolate, triangular on basal half; first recurrent vein meets the second cubital cell at apical third, and the second recurrent meets the third cubital cell beyond the middle; basal vein in fore wings basad of the transverse vein and the subdiscoidal in rear wings is basad of the cubitus; marginal cell rather long for the genus, three-fourths as long as its distance to wing tip; no spines on femora and only a very few on fore tibiae but the last two pair well spined, the spines over one-half as long as the diameter of tibiae; fore metatarsal joint with three comb spines more than twice length apart and longer than the width of joint; the second and third joints of fore tarsi each with a similar comb spine in middle; last two pairs of tarsi well spined; longer spur of posterior tibiae five-ninths as long as its metatarsal joint; ratio of lengths of joints of posterior legs femora through tarsi are as 45:50: 38: 19: 13: 6: 13.

Length: Head and thorax 5.65 mm, abdomen 5.0 mm, fore wing 7.9 mm, rear wing 6.5 mm.

Allotype female: Myrtle Beach, Horry Co., S. C. VIII-29, IX-6-49, David Shappirio (MCZ).

Paratypes: Ft. Washington, Md., VII-1-48 (RRD), Beltsville, Md., VIII-21-48 (Shappirio), Myrtle Beach, Horry Co., S. C., VIII-29, IX-9-49, David Shappirio (MCZ), Georgetown Co., S. C., IX-3-49 (Shappirio), Fond Parisien, Haiti, Feb. 11-18, 1922 alt. 60′ F. 4633 (Am. Mus. Nat. Hist.) and (R.R.D.), Cuba, S. of Pinar Rio, Sept. 12-23, 1913 (Am. Mus. Nat. Hist.)

The Fort Washington paratype is just about the size of the allotype but the other paratypes are much smaller; the difference in size of the various specimens is much greater than is generally the case and yet they are exactly similar in other respects except that the smaller specimens have much more red color on ventral surface of abdominal segments one and two. The size of the smallest paratype is: head and thorax 4.0 mm, abdomen 3.2 mm, fore wing 5.30 mm, rear wing 4.33 mm. This species is

very similar to *marginatus* but differs in the much stronger iridescent color of the wings. They are also darker in color, and there is much more red on base of the abdomen in both sexes. The males of *marginatus* and *reductus* generally do not have any red on the abdomen, while in this species the male has more red color than the female.

Since the paper on the genus *Pompilinus* (Dreisbach, 1949a) was written males of *P. insignis* (cr) and *P. coruscus* (cr) have come to hand and photomicrographs of the genitalia and last ventrite are shown in figs. 27, 29-31. I have not seen the types of these.

There are too many species here to be inserted in the key to the genus (Dreisbach, 1949a), and this will be added at a later date with other species from the Antilles and Mexico.

Pycnopompilus parvus n. sp.

Figs. 3, 4.

Holotype male.—Completely black, with a bluish or purplish reflection; numerous long hairs on head, vertex, clypeus, under clypeus, and very much heavier, longer ones under the head and neck, anterior edge and sides of fore coxae, pronotum, and propodeum; when seen from the side, the clypeus is almost flat, only a small part of front just back of antennae visible above the eye, eyes three times as broad as the posterior orbits; when seen from in front, the vertex is flat and at the same level as the eyes, except the ocellar triangle is raised slightly above the surface; fore ocellus about its diameter from the laterals and these not quite as far apart as their distance to the eyes; clypeus, face and inner orbits to above antennae with sericeous pubescence; ratio of lengths of the first four and last two antennal joints are as 40:14:40:35:40:30; pronotum angulate on posterior margin, propodeum with a slight sulcus; wings dark, almost black; marginal cell large about as long as its distance to wing tip; second and third cubital cells of almost equal size, the second almost rectangular; third cubital cell about one-half as long on marginal vein as on the cubitus; the two recurrent veins meet the second and third cubital cells at the apical fourth and the middle respectively; basal vein in fore wings basad of the transverse and the cubitous in rear wings is apicad of the subdiscoidal; no spines on fore femora and very few small ones on last two pair; fore tibiae with a few spines on ventral surface and the other two pair well spined; claws of fore legs cleft, with the other two pairs with a large tooth; longer spur of posterior tibiae two-thirds as long as its metatarsal joint; ratio of lengths of the joints of posterior legs femora through tarsi are as 40:48:28:10:8:4:18.

Length: Head and thorax 4.5 mm, abdomen approx. 4.5 mm, fore wing 7.0 mm, rear wing 5.3 mm, genitalia length 0.93 mm, width 0.79 mm, last ventrite length 0.99 mm, width 0.66 mm.

Holotype male: Kelton, Utah, VIII-24-49, G. F. Knowlton. (U.S.N.M.)

This species is distinct by virtue of the very narrow width of the apical portion of the volsellae as this is smaller than that of any other species. The last ventrite is almost of the same shape as that of *Pycnopompilus*

eureka (Banks), but the base is much broader, and the volsellae is much different.

In my paper on *Pycnopompilus* (Dreisbach, 1950) this species runs to couplet 4 and may be separated from the two species in that couplet, *P. eureka* and *P. arctus* as follows:

4a. Volsellae with the vertical part of hook at tip no wider than the rest of volsellae; numerous short hairs on parameres; face, clypeus, and inner orbits silvery pubescent; insect slightly bluish colored ..... *parvus* n. sp.
4a. Proceed as in second part of 4.

In the paper on *Pycnopompilus* (Dreisbach, 1950) the last ventrite labeled *P. lasiope*, fig. 41, was the last ventrite of *P. scelestus* (a duplicate of fig. 36). Fig. 20 is the last ventrite of *P. lasiope*. At the time this paper was written the last ventrite of *P. eureka* was not available and this is shown in fig. 21.

Anopompilinus arnaudi n. sp.

Figs. 1, 2

Holotype male.—Completely black, except a small reddish spot about the middle of the mandibles; beautiful, silvery pubescence on front, posterior orbits, ventral surface and sides of coxae, fore part of pronotum and on propodeum; a few long hairs on vertex, under clypeus and under side of head; when seen from the side, the clypeus has a slight bulge, the front from fore ocellus to antennae is slightly above the surface of eyes, the eyes are twice as broad as the posterior orbits; when seen from in front, the vertex is flat and on a plane with the eyes, the ocellar triangle visible above the surface, eyes approaching each other slightly at the clypeus; anterior ocellus its diameter from the laterals and these as far apart as their distance to eye margins; pronotum angulate on posterior margin, propodeum with a long dorsal surface, which is inclined; wings smoky beyond cells, but almost hyaline from cells to base; marginal cell very small only about one-third as long as its distance to wing tip; third cubital cell about one-half as long as the second cubital cell, both cells with the sides almost meeting on the marginal vein, slightly farther apart than the breadth of a vein; second recurrent vein meets the third cubital cell at the middle and the first recurrent vein beyond the center of the second cubital cell; basal vein basad of the transverse in the fore wings and the cubitus in rear wings is apicad of the subdiscoidal vein; very few spines on any part of the legs and these small, those on the tips of the tarsal joints are the longest; the claws on first pair of legs are cleft, those of the last two pair toothed; longer spur of posterior tibiae two-thirds as long as its metatarsal joint; ratio of lengths of the joints of last legs femora through tarsi are as 20:22:5:7:5:3:6.

Length: Head and thorax 2.6 mm, abdomen about 3.5 mm, fore wing 4.3 mm, rear wing 3.0 mm, genitalia length 0.66 mm, width 0.53 mm, last ventrite length 0.66 mm, width 0.38 mm.

Holotype male: Pinecrest, Tuolumne Co., Cal., VIII-12-48, P. H. Arnaud, Jr. The type will be deposited in Museum of Comparative Zoology at Harvard College.

This species is nearest to *A. anomalus* Dreisbach, as regards the genitalia, but the last ventrite is distinctly different as can be seen from the figure.

In my key to this genus (Dreisbach, 1949b), this species runs to the first part of couplet 8 (*A. anomalus* Dreis.) if the first clause is changed to read "marginal cell very small, at least two and one-half its length from the wing tip, and two to two and one-quarter times as long as wide." It can be separated from *A. anomalus* as follows:

8a. Apical third or less of last ventrite sloping outward from the abtuse tip and the sides of basal three fourths parallel; with a row of long hairs on basal half of last ventrite; second cubital cell one third as long on marginal vein as on the cubitus; first and second recurrent veins received by the second and third cubital cells at basal third and about the middle respectively ..... *anomalus*

8a. Apical half of last ventrite sloping outward to basal half in such a manner that the apical half of this narrowed part has the sides almost parallel; a short row of long hairs at base on each side, but not nearly so long a row as in preceding; second cubital cell only one fifth as long on marginal vein as on the cubitus, the second cubital cell hardly longer on the marginal vein than the third, the space between the sides on the marginal only about twice the thickness of a vein; the two recurrent veins received by the second and third cubital cells at the middle and beyond the middle respectively ..... *arnaudi*

The last ventrite of *Anopompilinus parvus* (Banks) was not available in my paper on this genus and is shown in fig. 12, also the photo of the genitalia of this species was very poor and a better one is shown in fig. 11.

Anoplius guatemalensis n. sp.

Figs. 18, 19.

Holotype male.—Black, with silvery pubescence at sides of antennal fossae with a few scattered white hairs on clypeus; a few upright hairs at base of clypeus, on mandibles, under head, on neck, and dense hair brushes on ventrites three through five, with those on four and five much denser than the one on three; when seen from the side there is a space between the brush on three and the one on four, but those on four and five are continuous; when seen from beneath at an angle, the hairs at sides are longer than the ones in the middle of segment; when seen from the side, the clypeus has a slight bulge about the center, vertex is on a level with the eyes, about one-half of front and antennal fossae above the surface of eyes, and the posterior orbits are less than half the width of eyes; when seen from in front, the eyes are plainly emarginate about the middle of front, in a long shallow curve, eyes at vertex the same distance apart as at the clypeus, vertex straight across with just an indication of a slight rise at the ocellar triangle; clypeus truncate in front; antennae rather thick and the eyes are large and prominent; ratio of lengths of first four joints of antennae (last two joints missing) are as 10:2:11:9; pronotum slightly angulate on posterior margin; propodeum in a smooth curve and without upright hair; wings black; marginal cell about its length from wing tip; the stigma is very short about one-half n marginal cell; second cubital cell almost quadrate, the third cell with the second and third intercubital veins about three times the thickness of a vein

apart on the marginal vein; first recurrent vein meets the second cubital beyond the apical third, and the second recurrent vein meets the third cubital at the middle; basal vein slightly basad of the transverse in the fore wings and the subdiscoidal vein ends beyond the cubitus, which is unusual in this genus; front coxae very large; very few spines on front legs, while the other two pair have the tibiae well spined, but the tarsi of all the legs have very few spines and these very small except at the tip of joints; claws all split and small spines under the last joint of all legs; longer spur of last tibiae about five-sevenths the length of its metatarsal joint; ratio of lengths of joints of posterior legs femora through tarsi are as 52:48:35:15:11:7:12.

Length: Head and thorax 5.6 mm, abdomen about 5.6 mm, fore wing 8.25 mm, rear wing 6.65 mm, genitalia length 1.06 mm, width 0.79 mm, last ventrite length 1.46 mm, width 0.73 mm.

Holotype male: Guatemala (MCZ).

This is a rather large, coarse appearing species with the eyes very large and prominent, emarginate in a broad, shallow curve. Genitalia is almost exactly like *A. illinoensis*, but the volsellae are not nearly so wide near the top and they extend outward farther in a slender process. It is also very much like *A. subtarsatus* n. sp. in the cobwebby like hair on the volsellae but again these extend outward in a narrow process unlike subtarsatus. The last ventrite differs from that of *illinoensis* in having the apical opaque tip only one-third the length of the ventrite, while in *illinoensis* this tip is fully one-half the length of the ventrite.

Anoplius subimbellis n. sp.

Figs. 23, 25.

Holotype male.—Completely black; very fine sericeous pubescence on clypeus, face, inner orbits to just above antennae, lower front corners of pronotum, and on propodeum; upright hair on mouth parts, clypeus, front, vertex, under head, and on propodeum; when seen from the side, the base of clypeus is on a lower plane than the rest of clypeus, almost as if a groove across base, whole front and vertex above surface of eyes, the nearer ocellus completely visible above the eye; posterior orbits very narrow, less than one-third as wide as eyes; when seen from in front the vertex is only slightly above the eyes, and a slight broad emargination on inner orbits about the center of front, eyes at vertex slightly farther apart than at clypeus; a short small impressed line from between antennae to about middle of front; ocelli in slight depressions, the fore ocellus about its diameter from the laterals and these about three fourths as far apart as their distance to eye margins; the first four and last two antennal segments have relative lengths of 35:11:40:35:25:32; joints not cylindrical but of slightly smaller diameter at the ends than in center; pronotum strongly angulate on posterior margin; fore wings almost hyaline to the cells, but cells and space beyond strongly yellowish, and no darker at tips than on cells; rear wings almost hyaline to the median cell and from there to tip as yellowish as the fore wings; the first

and second recurrent veins meet their respective cells at the apical two-fifths and in middle respectively; the third cubital cell open on the marginal vein about three times the width of a vein; in the fore wings the basal vein is basad of the transverse vein, and in rear wings the cubitus is very much apicad of the subdiscoidal vein; a few long hairs on the third ventrite but a very heavy hair brush on the fourth and fifth ventrites, which when seen from underneath appear hollow in the center due to the hairs becoming progressively shorter from the outer edge to middle; a few long hairs on fifth ventrite; the spines on legs and the split claws are typical of the genus; the longer spur of the posterior tibiae is nine-elevenths of its metatarsal joint; the comparative length of the joints of the posterior legs femora through tarsi are as 38:38:23:10:7:5:10.

Length: Head and thorax 3.98 mm, abdomen 3.64 mm, fore wing 6.60 mm, rear wing 4.64 mm, genitalia length 0.93 mm, width 0.66 mm, last ventrite length 0.99 mm, width 0.67 mm (at the widet part).

Holotype male: Falls Church, Va., VII-11, N. Banks (MCZ).

This species is very much like the species *A. imbellis* Banks and the variety *major* Dreisbach, but there are very distinct digerences. The volsellae is slightly different in shape than that of *imbellis* and the variety, and in the new species they are as long as the parapenial lobes whereas in the others they are much shorter. The parameres are also different, as in the new species the basal section (the base to the enlargement) is just about as long as the apical hairy section, whereas in *imbellis* and variety this section is only three-fifths as long as the apical portion. While the genitalia of all three species are of about the same size, the last ventrite of the new species is much larger than that of the other two. Since photos of the variety were not figured in the paper describing them (Dreisbach 1950) they are shown here in figs. 24, 26. Part of the stem of the last ventrite of the new species is broken off, but comparing the same parts of *imbellis* and the new species, they compare as follows:

	length	width
A. imbellis (L. Ventrite)	0.40 mm	0.59 mm
A. subimbellis (L. Ventrite)	0.66 mm	0.66 mm

In the key to the males of this genus (Dreisbach. 1950). *guatemalensis* runs to couplet 15, and *subimbellis* runs to couplet 16, and these two species may be incorporated in the keys as follows:

15a. As in 15 (1) ..... *subtarsatus*

15b. Volsellae not nearly so broad in the upper half and tapering to a rather long slender point, as long as the parapenial lobes; veins in rear wings not interstitial, the subdisocidal meets the disoidal beyond the origination of the cubitus; wings much blacker ..... *guatemalensis*

16a. Hair bands on sternites four to six inclusive; veins interstitial in the rear wings; volsellae with the upper half bare of hair; parameres very short. Western ..... *papago*

16b. Hair bands on sternites four and five very dense, and the hair bands continuous when the segments are in their usual position 17

17a. Wings deep brown all over but more so at tip; parameres long and pointed at inner upper end; veins in rear wings almost interstitial, and lobe of rear wing broad, obtuse at end, shorter than in the next species although the wings are longer; hair bands not appearing hollowed out in center when seen from beneath ..... *il inoen is*

17b. Wings only slightly brown to the cells, more so from cells to tip; parameres not long and pointed at inner upper end; cubitus in rear wings much beyond the subdiscoidal; anal lobe of rear wing narrow, almost pointed, and longer than in preceding species, comparative lengths 15:12; hair bands appear hollowed out in center when seen from beneath ..... *sub mb.llis*

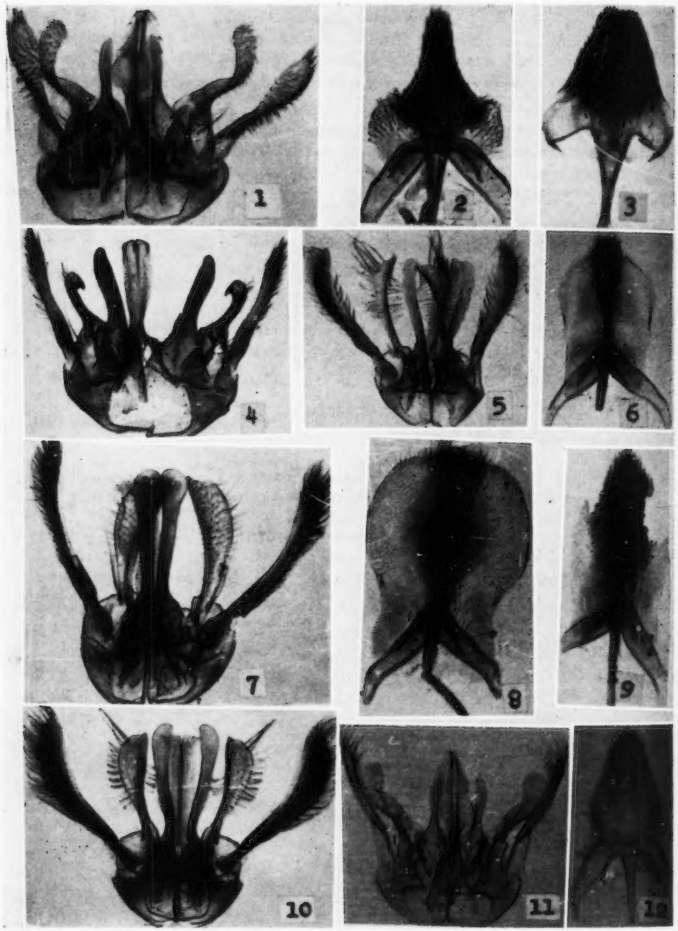
In the paper on *Anoplius* (Dreisbach, 1950), it was stated that *Anopl us bermudensis* was known in the female only. However, there is a male in the Harvard collection and photomicrographs of last ventrite and genitalia are shown in figs. 22, 28.

REFERENCES

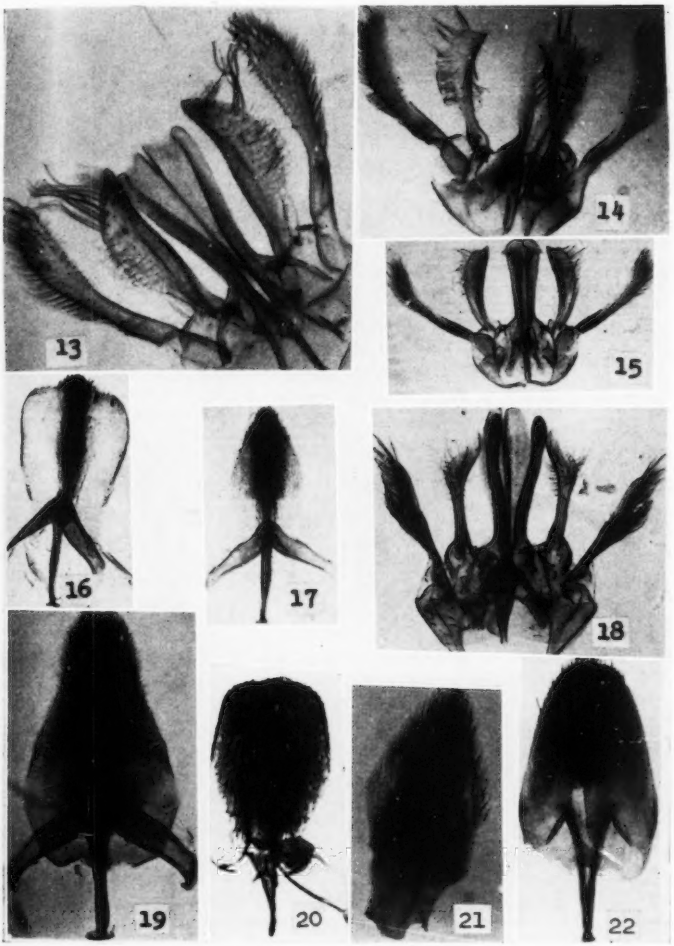
DREISBACH, R. R. 1949a--Psammocharini (Hymenoptera) of North America and the Antilles: Key to Genera; New Species and key to males of Pompilinus. Ent. Americana 29: 1-58.

———1949b—A new genus of the subfamily Psammocharinae (Hymenoptera) with descriptione of eight new species and a key to the species. Amer. Midl. Nat. 42 (3): 722-743.

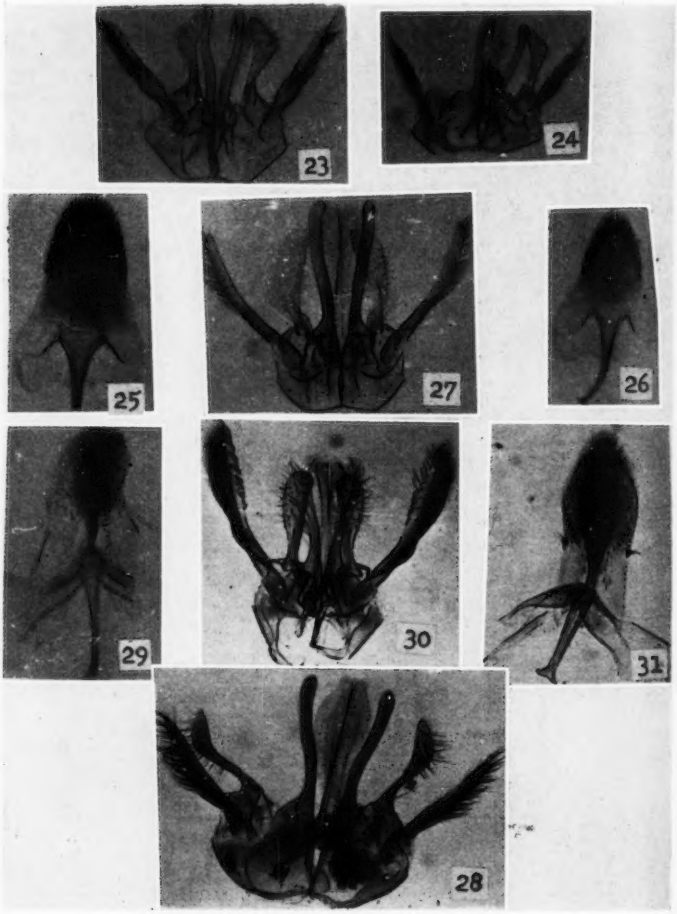
———1950—New species in the genera Anoplius, Pycnopompilus and Streptosella, n. gen. (Hymenoptera: Psammocharidae) with key to the males of N. America and the Antilles. Amer. Midl. Nat. 43 (3): 570-599.



Figs. 1-12.—1. *Anopompilinus arnaudi* n. sp., genitalia, ×60; 2. same, last ventrite, ×70; 3. *Pycnopompilus parvus* n. sp., last ventrite, ×41; 4. same, genitalia, ×40; 5. *Pompilinus shappirioi* n. sp., genitalia, ×40; 6. same, last ventrite, ×40; 7. *P. minutus* n. sp., genitalia, ×53; 8. same, last ventrite, ×56; 9. *P. basirufous* n. sp., last ventrite, ×40; 10. the same, genitalia, ×40; 11. *Anopompilinus parvulus* (Banks), genitalia, ×67; 12. same, last ventrite, ×57.



Figs. 13-22.—13. *Pompilinus texanus* Dreisbach, genitalia, ×56; 14. *P. submarginatus* n. sp., genitalia, ×50; 15. *P. utahensis* n. sp., genitalia, ×30; 16. same, last ventrite, ×44; 17. *P. submarginatus* n. sp., last ventrite, ×35; 18. *Anoplius guatemalensis* n. sp., genitalia, ×37; 19. same, last ventrite, ×40; 20. *Pycnopompilus lasiope*, last ventrite, ×42; 21. *P. eureka*, last ventrite, ×57; 22. *Anoplius bermudensis*, last ventrite, ×41.



Figs. 23-31.—23. *Anoplius subimbellis* n. sp., genitalia, ×35; 24. *A. imbellis major*, genitalia, ×40; 25. *A. subimbellis* n. sp., last ventrite, ×35; 26. *A. imbellis major*, last ventrite, ×40; 27. *Pompilinus insignis*, genitalia, ×38; 28. *Anoplius bermudensis*, genitalia, ×46; 29. *Pompilinus insignis*, last ventrite, ×38; 30. *P. coruscus*, genitalia, ×38; 31. same, last ventrite, ×38.

Types and Figured Specimens of Fossil Fishes in the Patten Collection, Dartmouth College Museum, Hanover, New Hampshire

Robert H. Denison

Chicago Natural History Museum, Chicago, Illinois

Professor William Patten, while perhaps best remembered at Dartmouth College for his stimulating and popular course on evolution, is most widely known in paleontological circles for his studies on the origin of vertebrates. In connection with his research he made a number of trips to various parts of the world, amassing an important collection of fossil fishes. The most outstanding part of the collection came from the Island of Oesel in the Baltic. Although Patten visited Oesel four times, the majority of his specimens were obtained on his last two expeditions in 1930 and 1932. The material he obtained here, totalling over 3500 specimens, is probably the largest and most representative collection of this early and primitive ostracoderm fauna, and includes a number of types and figured specimens. His collection from the Late Devonian of Escuminac Bay, Quebec, obtained between 1902 and 1912, is also notable, and includes exceptionally well preserved material of this famous and varied fauna. A brief trip to Spitsbergen in 1925 was not as productive as his other expeditions, and the limited materal he obtained has not been studied.

After Patten's death in 1932, his collections were studied by George M. Robertson and later by the author. Limited material has been and is being investigated on loan by Erik Jarvik in Sweden and by T. Stanley Westoll in England. In 1938 the collection was moved to the Dartmouth College Museum, where it was given the accession number 38-71, and recatalogued, using serial numbers in the museum's paleontology catalogue to replace the combination letter and number system employed by Patten and Robertson.

In view of the fact that the descriptions of Patten's collection have appeared in a variety of publications, it is desirable to bring together the information on the important specimens and their present catalogue numbers. The designation of types for the species described by Patten is another important function of this paper. After Patten's death, his later collections became incorporated with the original material upon which his descriptions were based. With the help of Dr. Robertson, it has been possible to separate the syntypic series, thus allowing the designation of lectotypes rather than neotypes. Revisionary notes on a number of species are also included.

References in the following list, except for the most recent papers, are to the full citations to be found in the following bibliographies:

Hay, O. P. 1929—Second bibliography and catalogue of the fossil Vertebrata of North America. Carnegie Inst. Washington, Publ. 390.

CAMP, C. L. ET AL. 1940, 1942, 1949—Bibliography of fossil vertebrates. Geol. Soc. Amer., Spec. Papers 27, 42, and Mem. 37.

Order OSTEOSTRACI

ATELEASPIS "n. sp." Patten

Late Devonian, Escuminac formation; Escuminac Bay, Quebec. 10086 Patten, W. 1912A: 357, 363, fig. 242.

This form is clearly distinct from the other Osteostraci reported from Escuminac Bay. It is larger than *Cephalaspis patteni* and *C. rosamundae*, the distance from the line connecing the anterior edge of the orbits to the anterior margin of the shield being 52 mm. The orbits are not shown on Patten's figure, although they are clearly indicated on the specimen, and have an approximate length of 19 mm. The anterior end of the nasohypophysial fossa may be seen slightly in advance of the orbits. A small area of the plates covering the dorsal field is preserved, but the extent and shape of the latter are not shown. The lateral fields may have extended well forward, but if so they are covered with plates that cannot be distinguished from the polygonal areas of the adjacent shield. The infraorbital sensory canal groove is partially and incorrectly shown by c^2 and c^3 of Patten's figure. The groove labelled c^1 by Patten corresponds to the anterior marginal of *Trematapsis* and *Thyestes*. The ventral marginal rim, as is shown by its impression, was ornamented with small distinct tubercles. The dorsal exoskeleton is covered with small, round-topped, widely scattered tubercles, apparently capped with enamel and dentine. Between the tubercles the skeleton is thin due to the absence of the superficial layer and the outer part of the middle layer. In these regions the lower part of the middle layer forms the surface of the exoskeleton, and shows distinct radiating canals. The latter, as is often the case in *Cephalaspis*, are arranged in polygons that Patten believed to represent separate plates.

This form, as far as it is known, could belong to *Cephalaspis*, but its incompleteness makes this difficult to demonstrate. In the absence even of distinct generic characters, it is considered undesirable to attempt to define a new species based upon it.

CEPHALASPIS ACADICA Robertson

Middle (?) Devonian, Gaspé sandstone; Campbellton, New Brunswick. 10082 (C-3) —*Holotype*. Robertson, G. M. 1936A: 293, fig. 4.

CEPHALASPIS CANADENSIS Robertson

Middle (?) Devonian, Gaspé sandstone; Campbellton, New Brunswick. 10081 (C-2) —*Holotype*. Robertson, G. M. 1936A: 292, fig. 3.

Judging by the matrix and the manner of preservation of the bone, L. S. Russell (in litteris, 1946) believes that the holotypes of *Cephalaspis acadica* and *C. canadensis* came from near a river beach at a railway cut west of Campbellton station. Because of the distortion that is evident in most specimens from this locality, differences in shape and proportion cannot be relied on to distinguish these species, as has been demonstrated by stretching rubber impressions of them. This leaves no important or reliable feature to distinguish these species from each other, or from *C. campbelltonensis* Whiteaves, except perhaps for the larger size of the latter.

CEPHALASPIS PATTENI Robertson

Late Devonian, Escuminac formation; Escuminac Bay, Quebec. 10080 (C-1)—*Holotype*. Robertson, G. M. 1936A: 288, 289, 295, figs. 1-2.

This species is doubtfully distinct from *C. laticeps* Traquair.

DARTMUTHIA GEMMIFERA Patten

Late Silurian, Ludlow (K_1); Atla, Island of Oesel. 8553 (A-70)—*Lectotype*. Patten, W. 1931A: 672. Robertson, G. M. 1935A: 324-334, fig. 2.

In the absence of any previously designated type, this specimen is selected as lectotype.

8554 (A-71) Robertson, G. M. 1935A: fig. 1. 8568 (A-85) Robertson, G. M. 1935A: fig. 3. 8589 (A-106) Robertson, G. M. 1935A: fig. 4. Specimen not identified (not A-94). Idem., fig. 5.

OESELASPIS PUSTULATA (Patten)

Late Silurian, Ludlow (K_1); Atla, Island of Oesel. 9198 (D-2)—*Lectotype.* Patten, W. 1931A: 672 (*Didymaspis*). Robertson, G. M. 1935B: 453-461, fig. 2. (Referred to *Oeselaspis*, gen. nov.).

In the absence of any previously designated type, this specimen is selected as lectotype.

9199 Robertson, G. M. 1935B: fig. 1. 9208 Robertson, G. M. 1935B: fig. 3. 9209 Robertson, G. M. 1935B: fig. 4.

PROCEPHALASPIS OESELENSIS (Robertson)

Late Silurian, Ludlow (K_1); probably Atla, Island of Oesel. 12657 (C-10)—*Holotype.* Robertson, G. M. 1939B: 360-361, fig. 1 (*Cephalaspis*). Denison, R. H. 1951. Fieldiana, Geol. 11(3): 189 (Referred to *Procephalaspis*, gen. nov.).

12668 (C-100) Robertson, G. M. 1939B: fig. 2.

ROTSIKÜLLASPIS OBRUTCHEVI Robertson

Late Silurian, Ludlow (K_1); Wita quarry, near Rotsiküll, Island of Oesel. 9404 (T-135)—*Holotype.* Robertson, G. M. 1938D: 490-493, pl. 60, fig. 5. Denison, R. H. 1951. Fieldiana, Geol. 11(3): 158-159 (Referred to *Saaremaaspis mickwitzi*).

The following specimens figured as *Rotsiküllaspis obrutchevi* also belong to *Saaremaaspis mickwitzi:* 9402 (T-133) Robertson, G. M. 1938D: pl. 60, fig. 4. 9551 (T-283) Robertson, G. M. 1938D: pl. 60, figs. 1, 6. 12775 (T-577) Robertson, G. M. 1938D: pl. 60, fig. 3.

SAAREMAASPIS MICKWITZI (Rohon)

Same horizon and locality: 9526 (T-258) Robertson, G. M. 1938D: 489, pl. 60, fig. 7.

TREMATASPIS MAMMILLATA Patten

Late Silurian, Ludlow (K_1); Atla, Island of Oesel. 9713 (T-445)—*Lectotype.* Patten, W. 1931A: 672. Robertson, G. M. 1938A: 289, pl. 2, fig. 3 (Designates this specimen as lectotype).

9417 (T-148) Robertson, G. M. 1938A: pl. 1, fig. 3. 9678 (T-410) Robertson, G. M. 1938A: pl. 1, fig. 4. 9687 (T-419) Robertson, G. M. 1938A: pl. 1, fig. 6.

TREMATASPIS MILLERI Patten

Late Silurian, Ludlow (K_1); Atla, Island of Oesel. 9813 (T-546)—*Lectotype.* Patten, W. 1931A: 672. Robertson, G. M. 1938A: 289, pl. 2, fig. 2 (Designates this specimen as lectotype).

9420 (T-151) Robertson, G. M. 1938A: pl. 3, fig. 1.

TREMATASPIS PANDERI Robertson

Late Silurian, Ludlow (K_1); probably Atla, Island of Oesel. 9544 (T-276)—*Holotype.* Robertson, G. M. 1938A: 290, pl. 2, fig. 5. Denison, R. H. 1947. Amer. Jour. Sci. 245: 363 (Referred to *T. mammillata*). Robertson, G. M. 1950. ibid. 248: 342 (see note below under *T. scalaris*).

TREMATASPIS PATTENI Robertson

Late Silurian, Ludlow (K_1); probably Atla, Island of Oesel. 9793 (T-526)—*Holotype.* Robertson, G. M. 1938A: 290, pl. 2, fig. 7. Denison, R. H. 1947. Amer. Jour. Sci. 245: 358 (Referred to *T. mammillata*). Robertson, G. M. 1950. ibid. 248: 341 (Concedes "that *T. patteni* may be based on immature specimens" of *T. mammillata*, but "believes it wiser to retain the species."

TREMATASPIS ROHONI Robertson

Late Silurian, Ludlow (K_1); Island of Oesel. 9379 (T-106)—*Holotype.* Robertson, G. M. 1938A: 289-290, pl. 2, fig. 4, text-fig. 3. Denison, R. H. 1947. Amer. Jour. Sci. 245: 347, fig. 7B.

TREMATASPIS SCALARIS Robertson

Late Silurian, Ludlow (K_1); probably Atla, Island of Oesel. 9828 (T-561)—*Holotype*. Robertson, G. M. 1938A: 290, pl. 2, fig. 8. Denison, R. H. 1947. Amer. Jour. Sci. 245: 362-363 (Referred to *T. mammillata*). Robertson, G. M. 1950. ibid., 248: 342 (Is not convinced that the peculiar shield markings that he used to distinguish *T. panderi* and *T. scalaris* "might not have been permanent markings of a variant form rather than anomalous characters of *T. mammillata.*")

TREMATASPIS SCHMIDTI Rohon

Late Silurian, Ludlow (K_1); probably Wita Quarry, near Rotsiküll, Island of Oesel. 9409 (T-140) Robertson, G. M. 1938A: pl. 2, fig. 9. 9410 (T-141) Robertson, G. M. 1938A: pl. 2, fig. 1.

TREMATASPIS sp.

Late Silurian, Ludlow (K_1); Island of Oesel.

9383 (T-110) Robertson, G. M. 1938A: pl. 1, figs. 1-2. 9520 (T-252) Robertson, G. M. 1938A: pl. 1, fig. 5. 9602 (T-334) Robertson, G. M. 1938A: pl. 2, fig. 6. 9626 (T-358) Robertson, G. M. 1938A: pl. 3, fig. 7. 9819 (T-552) Robertson, G. M. 1938A: pl. 3, fig. 2. 12779 (T-570) Patten, W. 1903A: figs. 1-3, 9b. Patten, W. 1912A: figs. 241 c, d, e. Robertson, G. M. 1938A: pl. 3, figs. 3-4. 12780 (T-.....) Patten, W. 1903A: fig. 9a. 12781 (T-572) Patten, W. 1903A: figs. 4-6. Patten, W. 1912A: fig. 240. Robertson, G. M. 1938A: pl. 3, figs. 5-6.

WITAASPIS PATTENI Robertson

Late Silurian, Ludlow (K_1); Wita quarry, near Rotisküll, Island of Oesel. 12714 (C-15)—*Holotype*. Robertson, G. M. 1940A: 297-298. Denison, R. H. 1951. Fieldiana, Geol. 11(3): 157-158 (Referred to *W. schenkii*).

WITAASPIS SCHRENKII (Pander)

Late Silurian, Ludlow (K_1); Wita quarry, near Rotsiküll, Island of Oesel.

12722 (C-16) Robertson, G. M. 1939A: fig. 3. (*W. schrenckii*). 12733 (C-28) Robertson, G. M. 1939A: fig. 4. (*W. schrenckii*). 12734 (C-29) Robertson, G. M. 1939A: fig. 2. (*W. schrenckii*). 12746 (C-42) Robertson, G. M. 1939A: fig. 5. (*W. schrenckii*). 12750 (C-49) Robertson, G. M. 1939A: fig. 6. (*W. schrenckii*).

Order ANASPIDA

SAAROLEPIS OESELENSIS (Robertson)

Late Silurian, Ludlow (K_1); Island of Oesel. 12648 (An-1)—*Holotype*. Robertson, G. M. 1941B: 315 (*Anaspis*, name preoccupied). Robertson, G. M. 1945. Jour. Pal. 19: 77 (Referred to *Saarolepis*, new name).

Order ANTIARCHI

BOTHRIOLEPIS CANADENSIS Whiteaves

Late Devonian, Escuminac formation; Escuminac Bay, Quebec.

10303 Patten, W. 1912A: fig. 252A. 10309 Patten, W. 1912A: fig. 252B. 10600 Patten, W. 1912A: fig. 250D. 10637 Patten, W. 1912A: fig. 249. 10656 Patten, W. 1912A: fig. 250 A, B. 10698 Patten, W. 1912A: fig. 250 C. 10813 Patten, W. 1912A: fig. 257. 10814 Patten, W. 1912A: fig. 257.

Order CROSSOPTERYGII

EUSTHENOPTERON FOORDI Whiteaves

Late Devonian, Escuminac formation; Escuminac Bay, Quebec.

12782 (F-1) Jarvik, E. 1944. K. Svensk. Vetensk. Akad. Handl., (3), 21(7), fig. 2 A. 12785 (F-4) Patten, W. 1912A: fig. 265 A. 12786 (F-5) Jarvik, E. 1942: pl. 6, fig. 2; pl. 9, fig. 1; pl. 10. Jarvik, E. 1944. K. Svensk. Vetensk. Akad. Handl, (3), 21(3), figs. 5 E, J. 12792 (F-11) Jarvik, E. 1944. Idem., fig. 6B.

The Relationship of the Chorus Frogs, Pseudacris nigrita feriarum and Pseudacris n. triseriata

Philip W. and Dorothy M. Smith
Illinois Natural History Survey, Urbana

Early in the development of a project directed toward a survey of the herpetofauna of Illinois, extensive field work and the accumulation of specimens from widespread localities in the state revealed that the Illinois populations of chorus frogs, *Pseudacris nigrita*, consisted of two geographic races, differing in structure, markings, and habits. Attempts to allocate these populations correctly further revealed the literature involving the *nigrita* complex of the genus to be in a state of confusion, almost paralleling that in *Rana pipiens*.

This strictly North American genus occurs from Great Slave Lake and Hudson Bay south to northern Arizona and the Gulf of Mexico and east to New York and Florida. Two well defined complexes are present in the genus, the *ornata-streckeri* group and the *nigrita* group. The latter complex, whose range encompasses that of the entire genus, contains three forms (*brachyphona, brimleyi,* and *clarkii*) generally, and probably correctly, assigned to specific rank. The remaining five forms (*verrucosa, nigrita, feriarum, triseriata,* and *septentrionalis*) have been variously assigned and there is little agreement among present day authors on the proper ranks, ranges, and even the validity of certain of them. The most recent arrangement (Wright & Wright. 1949) which began with the third edition of the check-list (Stejneger & Barbour, 1933) recognizes all five as subspecies of *Pseudacris nigrita*. Data from the present study indicate that they are subspecies of a single species, thus supporting the Wrights' views. Although only two subspecies are treated here in detail, the following key has been prepared for all *P. nigrita* subspecies.

KEY TO THE SUBSPECIES OF PSEUDACRIS NIGRITA

1. Tibial length usually 47% or more of snout-vent length 2
   Tibial length usually less than 47% of snout-vent length 4

2. Dorsal pattern of many small spots; often warty; snout acuminate; habitus distinctly *Acris*-like 3
   Dorsal pattern striped, plain, or consisting of broken stripes but not with small, rounded spots; seldom warty; snout broad; habitus not *Acris*-like (see fig. 2) ..... *feriarum*

3. Light unbroken stripe along margin of upper jaw ..... *nigrita*
   (Coastal plain from North Carolina to northern Florida and west along Gulf coast to Pearl River, Mississippi).
   A row of light spots on the margin of the upper jaw ..... *verrucosa*
   (Peninsular Florida).

4. Tibia/body ratio usually less than 41%; head narrow; snout depressed .... *septentrionalis* (Yukon and Hudson Bay south to central Minnesota and down Rocky Mountains at high elevations).

Tibia/body ratio usually more than 41%; snout usually conical (see fig. 2) .... *triseriata*

It was soon apparent that the southern Illinois series of chorus frogs were identical in all essential characters with those of the lower Mississippi Valley and both were indistinguishable from *Pseudacris n. feriarum*, which is currently regarded as being restricted to the Piedmont Plateau. This situation invited an inquiry into the systematic status of this race and its relationships to *Pseudacris n. triseriata*. The examination of material from over most of the United States and Canada has necessitated rediagnosis of the subspecies and redefinition of their ranges, resulting in certain changes in concepts of these forms. Usage of subspecific names in the following pages is in accordance with these changes.

METHODS

In order to establish characters for the separation of *P. n. feriarum* and *P. n. triseriata*, ratios of various parts of the body have been determined and tested. The most useful of these is the tibia/body ratio described by Schmidt (1938, pp. 378-380). This ratio is obtained by dividing the over-all length of the flexed tibia by the snout-vent length. Other useful characters are the length and width of the head in relation to the body length. These are similarly computed and also expressed as percentages. Head length represents the distance from the tip of the snout to the posterior border of the tympanum; head width, the width at the widest portion (at the angle of the jaws). These ratios all exhibit overlap but differ in their averages. Coloration and pattern, while reliable in fresh material, have been used to a minimum degree as markings are often indiscernible on old alcoholic specimens.

Ranges, intergrading areas, and clines were found by plotting means (when two or more frogs were available from a locality) of body proportions on a large, county outline map. Samples representing essentially like, and therefore probably interbreeding, populations were lumped and the mean and standard deviation computed for each unit. N-1 was substituted for N throughout to correct for the small sizes of the samples. Various units (exclusive of intergrades) were compared and the standard error of the difference tested. No attempt has been made to locate all published records and no records from the literature have been plotted on the map.

ACKNOWLEDGMENTS

We are grateful to Dr. Hobart M. Smith for guidance throughout this study and for his advice on the numerous problems that arose during the course of the work. We wish also to thank Dr. J. B. Kitzmiller for aid with statistical analyses of several large samples which were used. Dave A. Langebartel, W. Leslie Burger, and J. C. List have assisted in locating material for examination. We are indebted to the following museum officials for their kindness in lending specimens for study: R. J. Baldauf, S. C. Bishop, C. M. Bogert, W. J. Breckenridge, B. C. Brown, G. C. Carl, D. M. Cochran, H. K. Gloyd, B. M. Hecht, E. B. S. Logier, J. E. Moore, A. I. Ortenburger, C. H. Pope, K. P. Schmidt, H. C. Seibert, B. Shreve, H. K. Suzuki, E. H. Taylor, and G. L. Ward.

Thanks also are due to E. L. Bell, B. C. Brown, R. A. Edgren, S. A. Minton, F. A. Shannon, P. Swanson and L. W. Wilson for specimens loaned from their personal collections.

Sources of material examined are abbreviated as follows:

AMNH—American Museum of Natural History
BCB—Bryce C. Brown
BUM—Strecker Museum, Baylor University
CAS—Chicago Academy of Sciences
CNHM—Chicago Natural History Museum
ELB—Edwin L. Bell
EC—Earlham College, Richmond, Indiana
FAC—Fannye A. Cook
HKS—Howard K. Suzuki
INHS—Illinois Natural History Survey
KU—University of Kansas Museum of Natural History
LLW—L. Wayne Wilson
MCZ—Museum of Comparative Zoology
MPM—Milwaukee Public Museum
OU—University of Oklahoma Museum of Zoology
OS—Ohio University at Athens
ROM—Royal Ontario Museum
RM—Reading Museum, Reading, Pa.
SAM—Sherman A. Minton, Jr.
UIMNH—University of Illinois Museum of Natural History
UM—University of Minnesota Museum of Natural History
UR—University of Rochester Museum of Natural History
USNM—United States National Museum

PSEUDACRIS NIGRITA FERIARUM (Baird)

Helocaetes feriarum Baird, 1854, pp. 59-60. *Pseudacris feriarum*, Cope, 1862, p. 157. *Chorophilus feriarum*, Cope, 1889, pp. 339-341. *Chorophilus nigritus feriarum*, Dickerson, 1908, pp. 157-160. *Hyla feriarum*, Noble, 1923, p. 5. *Pseudacris nigrita feriarum*, Wright and Wright, 1933, pp. 90-91. *Chorophilus triseriatus corporalis* (nomen nudum) Cope, 1875, p. 30. *Pseudacris nigrita triseriata* (*nec* Wied), Burt, 1938, p. 342.

Type locality.—Carlisle, Cumberland Co., Pennsylvania.

Range.—Northern New Jersey and southeastern Pennsylvania south to central North Carolina and southwest to eastern Texas and southeastern Oklahoma (see fig. 2).

Diagnosis.—A subspecies of *P. nigrita* with a dorsal pattern varying from distinct longitudinal stripes to speckled or even plain; most often dorsal stripes either much interrupted or very narrow and not extending from orbital region all the way to the vent; lateral stripes nearly always prominent, often accentuating weakness of dorsal pattern; ground color fawn, gray, tan, or even pink with stripes or flecks of brown, black, or olive; venter cream colored, usually with dark stippling on breast; upper parts of limbs lightly speckled, dashed, or plain; upper jaw with a light stripe, narrowly margined below with dark; triangle usually present between eyes; tibial length usually more than 47% of snout-vent length (averaging 50.6%); femora and feet proportionately long; head length/body length ratio varying from 29% to 40%, averaging 33.7%; head width/body length ratio ranging from 26% to 36%, averaging 31.8%; snout broad and not attenuated; eyes large and lateral in position; digital pads distinctly wider than penultimate phalanx although much smaller than in *Hyla;* back smooth to evenly granular; venter granular or pustular, the pustules extending onto the gular region.

Comparisons.—*Pseudacris nigrita feriarum* differs from *P. n. nigrita* by the stouter body, broad head without an acuminate snout, granular or smooth

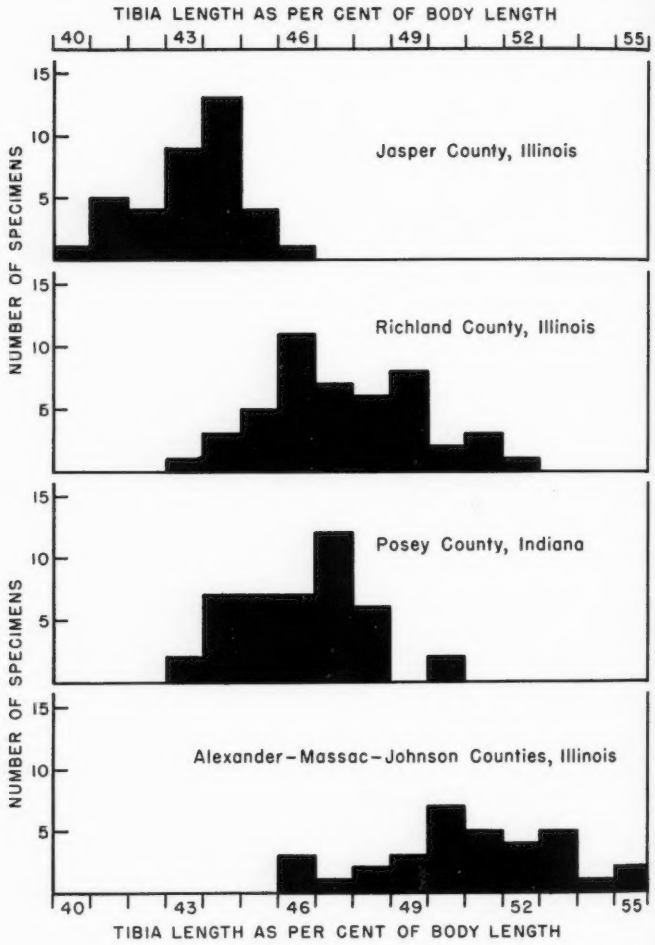


Fig. 1.—Tibia-body length relationships

skin, and by the absence of small round spots dorsally. It can be separated from *triseriata* by the longer limbs (tibia equals half the body length), the proportionately larger eyes, broader head, larger digital pads, and weak dorsal pattern.

Differences in habits and habitat preference are also apparent between *triseriata* from northern and central Illinois and *feriarum* from southern Illinois. That *triseriata* is almost impossible to collect except in the breeding pools is known to every herpetologist. This is probably because these frogs disperse widely on the prairie, hiding among weeds and in cracks in the ground. In southern Illinois, on the other hand, chorus frogs may be collected successfully throughout the summer in densely shaded flood-plain forests where they perch on the scant vegetation much in the manner of *Hyla crucifer*. The more arboreal habits of *feriarum* are suggested by the larger toe pads and longer legs. The differences in habits are apparently due to the correlation of relative leg length and the size of the leaps and manner of walking, *feriarum* being able to leap much farther than *triseriata*. Specimens of the latter race, although capable of short, rapid hops, are more prone to walk rapidly when disturbed. The shortened tibiae barely raise the body off the ground, and the rapid walking appears much like that of some miniature mammal.

Series of *feriarum* from the Piedmont have been compared with material from the lower Mississippi Valley and no consistent characters found to separate them. The western *feriarum*, exclusive of intergrades, were found to have a tibia/body ratio mean of $50.48 \pm .298$. A sample of east coast *feriarum*, exclusive of intergrades, exhibits a mean of $51.34 \pm .370$. The mean difference is thus only .86; the standard error of the difference is .471, giving a t value of 1.82.

Comparison of a sample of lower Mississippi Valley *feriarum*, which has heretofore been called *triseriata*, with a sample of non-intergrading *triseriata* (central Illinois and eastern Kansas), however, shows a mean difference of 7.9, standard error of the difference of .314 and a t value of 24.9. The difference here is obvious.

Remarks.—Taxonomically no subspecies of North American hylid has had a more confused history, despite the fact that in many areas individuals of this race are extremely abundant. This confusion is probably the result of a combination of facts: the wide range of variation found in specimens at the periphery of the range as in New Jersey, the presumed occurrence of this race in geographically distinct areas as in Arkansas and northwest Florida, the chaotic nature of intergrades in the intergrading areas, the absence of museum specimens from the mid-south, and because no one reviewer has had sufficiently large series from both the Piedmont and the lower Mississippi Valley for comparison. Cope (1889, pp. 339-341) apparently was familiar with western *feriarum* and allocated specimens from southern Indiana and southeastern Illinois to this subspecies. For reasons unknown to us Stejneger & Barbour (*loc. cit.*) and others at about the same time restricted *feriarum* to the Piedmont region and authors since, with a few exceptions, have followed suit.

Principal among those disregarding this restriction of *feriarum* were Taylor (1935, p. 209) who correctly assigned Lafayette County, Arkansas, specimens; Burt (1938, p. 342) who could find nothing to separate Piedmont Carolina *feriarum* from the so-called *triseriata* farther inland; and Cagle (1942, p. 180) who properly assigned frogs from Union and Jackson counties, Illinois, to *feriarum*.

Other comments and arrangements are of interest. Wright and Wright (1949, pp. 253-258) question the distinctness of eastern and western *feriarum* and also the distinctness of *triseriata* from *feriarum* in certain areas. Other authors have noted similarities or differences, directly or indirectly, which have some bearing on the question. Schmidt (*op. cit.*) states: "Here [south to north in Illinois] the variation is far from regular. . . . The discontinuity between the frogs from southern and northern Illinois suggests a taxonomic change." Smith (1947, p. 183) notes that Brazos County, Texas, material varies from Kansas *triseriata* in distinctness of the lines and that some examples appear unicolorous. Bragg (1948, pp. 149-168) has noted similar differences between Oklahoma populations. Conant (1945, p. 3; 1947, p. 25) allocated "Del-Mar-Va"* specimens to *triseriata*. It may be that the Del-Mar-Va frogs are shorter legged than Piedmont *feriarum*, like those in New Jersey.

The occurrence of this subspecies within the presumed range of *P. nigrita* led Carr (1940, pp. 56-57) and other recent authors to believe that *feriarum* should be given specific rank. Most striking example of such an apparent overlap in range without loss of identity of the forms involved is the Liberty County, Florida, population of *P. n. feriarum* reported by Carr (*ibid.*). This contention has been greatly weakened by Neill (1949, pp. 227-228) who points out that the intergrading area between *feriarum* and the typical subspecies extends southwestward from Richmond County, Georgia, into western Florida. We have not seen Carr's specimens but a series of very typical *feriarum* from Stewart County, Georgia, indicates this to be true. Whether the range of *nigrita* is confined to a narrow strip of coast eastward to the Pearl River, Mississippi, or whether it extends inland in southern Alabama and Mississippi could not be ascertained as specimens from these areas were not available to us. On the east coast the typical subspecies replaces this race at about the fall line from central North Carolina southward. The western limit of range of the race appears to extend from Centre County, Pa., southwest to extreme southeastern Kentucky and thence west to southern Illinois, southeastern Oklahoma, and east Texas. Too few specimens have been available to us to determine the range of the species in central Tennessee (fig. 2). Intergradation with *P. n. triseriata* occurs in northwestern Kentucky, southern Indiana, southern Illinois, northern Arkansas, and northern and central Oklahoma. Central and northeastern Kentucky, western West Virginia, southeastern Ohio, and southwestern Pennsylvania appear to be a hiatus between the two races but is occupied by the allopatric *P. brachyphona*. Hybridization between these species has not, so far as we are aware, been reported.

* The peninsula east of Chesapeake Bay.

TABLE 1.—Summary of variation in tibial lengths of *Pseudacris n. feriarum* expressed in percentages (exclusive of intergrading populations).

	New Jersey	Eastern W. Va.	Central Pa.	South Ill.	La.	East Texas
No. of specimens	24	110	36	33	33	49
Extremes	42–50	44–54	46–54	43–57	43–55	42–53
Mean	46.5	49.5	50.0	51.0	49.2	47.0

Variation.—Table 1 sums up the major geographical variation. It may be seen that Louisiana series actually average somewhat less in leg length than do series from southern Illinois, and thus do not parallel the situation Schmidt (*op. cit.*) finds in *Rana sylvatica*. On the other hand, at both the eastern and western limits of the range, the populations show a tendency toward shorter legs, in every way resembling intergrading populations of *feriarum* and *triseriata*. These populations are not intergrades in the usual sense of the word, for in neither case is there an annectant race through which the two blend. From southern Indiana to northern Oklahoma the same tendency toward shortened limbs is seen, but here the populations actually are intergrades, blending with the adjacent *triseriata*. Thus the populations at the eastern and western limits of the range of the subspecies must be considered as peripherally varying *feriarum* since elsewhere in the range this character is rather constant. As will be seen later this manner of variation is also found in *triseriata*, and a more complete discussion is included for that subspecies.

Pseudacris nigrita feriarum examined:

ALABAMA: *Jackson Co.* Stevenson (AMNH 1000). *Montgomery Co.* 4 mi. NE Waters (USNM 99581). *Calhoun Co.* Ft. McClellan (AMNH 51671 (3)).

ARKANSAS: *Clark Co.* (CNHM 30539). *Drew Co.* (CNHM 31632, 35541, 40793). *Hempstead Co.* Fulton (AMNH 52503). *Lafayette Co.* Lewisville (KU 11699-01). *White Co.* (KU 17519, 17679).

GEORGIA: *De Kalb Co.* Decatur (MCZ 19306-10). *Fulton Co.* (MCZ 17319-20). *Stewart Co.* 8 mi. NW Lumpkin (SAM A-51 (3)).

ILLINOIS: *Alexander Co.* Horseshoe Lake (CNHM 41266; INHS 5125-7, 2275); Olive Branch (CNHM 2170); Unity (INHS 3337). *Gallatin Co.* 2 mi. S Shawneetown (INHS 5055). *Jackson Co.* 12 mi. SW *Murphysboro* (INHS 2543). *Johnson Co.* Vienna (INHS 2497-8, 2490-4). *Massac Co.* (INHS 2222); 18 mi. S Renshaw (INHS 4897-901). *Pope Co.* Rosiclair (INHS 2945); 2 mi. W Golconda (INHS 4902-6). *Saline Co.* (UIMNH 793; INHS 4895-6). *Union Co.* Alto Pass (UIMNH 1792-3); Jonesboro (CNHM 18593, 18596, 38707, 18630-1; CAS 2016-9); 3 mi. S Ware (CAS 10902).

KENTUCKY: *Bell Co.* Middleboro (CAS 13933-4). *Carlisle Co.* 3 mi. N Bardwell (USNM 85584). *Trigg Co.* 5 mi. NE Golden Pond (USNM 106268).

LOUISIANA: ——(AMNH 50131). *Baton Rouge Par.* Baton Rouge (UIMNH 31565-6). *Caddo Par.* Shreveport (MCZ 21870-1). *Darahan Par.* (AMNH 51922-3). *De Soto Par.* 18 mi. S Shreveport (AMNH 37106-7). *Jefferson Par.* Marrero (MCZ 21868). *Madison Par.* (USNM 18388-90). *Natchitoches Par.* Steep Hill Creek (KU 24462). *Orleans Par.* New Orleans (AMNH 6391). *Ouachita Par.* (OU 25120-31); Monroe (AMNH 51876). *St. Charles Par.* 27 mi. W New Orleans (AMNH 45110). *St. Tammany Par.* Slidell (MCZ 11832-3; KU 3451-2).

MARYLAND: *Frederick Co.* (OU 24715). *Montgomery Co.* (CNHM 51931-5). *Prince Georges Co.* (USNM 9667). *Queen Anne Co.* Laurel (CNHM 6917).

MISSISSIPPI: *Hinds Co.* Clinton (AMNH 46004-12). *Lauderdale Co.* (FAC 1252). *Noxubee Co.* Brooksville (MCZ 21175-9).

NEW JERSEY: *Bergen Co.* Oradel (AMNH 51666); 1 mi. N Oradel (AMNH 35497-8); Leonia (AMNH 15505); Harrington Beach (AMNH 22951-3, 34734-6, 50133-4). *Burlington Co.* Centerton (AMNH 51664). *Essex Co.* Caldwell (AMNH 11315, 11321-2). *Mercer Co.* Bet. Trenton and Moorestown (AMNH 51667). *Middlesex Co.* Metuchen (AMNH 3809). *Ocean Co.* opposite Seaside Hts. (AMNH 43510-12); north of Lakewood (AMNH 51660); 4 mi. W Seaside Hts. (AMNH 51663). *Sussex Co.* Little Falls (AMNH 16812).

NORTH CAROLINA: *Durham Co.* (USNM 91564). *Wake Co.* Raleigh (UIMNH 1 sp.; CNHM 1992; AMNH 5799-800, 24006, 3094); 10 mi. E Raleigh (AMNH 33311).

OKLAHOMA: *Delaware Co.* 2 mi. W Ark. line (OU 23715); *La Flore Co.* Heavener (OU 23723). *McCurtain Co.* Idabel (OU 23668-75, 23590); 6 mi. N Idabel (OU 23962); 1.8 mi. E Harris (OU 23697-9).

PENNSYLVANIA: *Berks Co.* N of Elverson (RM 2 sp.); *Huntingdon Co.* NE McAlevys Fort (EB 26 sp.; INHS 4165-74).

SOUTH CAROLINA: *Greenville Co.* Greenville (USNM 71768-72).

TENNESSEE: *Obion Co.* Reelfoot Lake (UIMNH 798-9, 1794). *Sevier Co.* Greenbriar (CAS 7992-8000).

TEXAS: *Bowie Co.* Sulphur River (BUM 3508, 3510-1, 3513-4, 3516-7, 3519-21, 3524, 3527, 3529-31). *Brazos Co.* College Station (BCB 1129, 1132, 1134-6, 1138, 1140-3, 1145-9, 1151-5, 1511, 1513, 1515, 1323-4, 1768, 2027, 3483). *Burleson Co.* Grant (BCB 1784). *Cooke Co.* Gainesville (USNM 14522). *Dallas Co.* Dallas (USNM 89915). *Hardin Co.* Saratoga (UIMNH 795). *Harrison Co.* Lake Caddo (AMNH 12878-9). *McLennan Co.* Waco (AMNH 24007). *Polk Co.* Livingston (BCB 3698).

VIRGINIA: *Fairfax Co.* McVernon (AMNH 32877); Arlington (USNM 45965).

WEST VIRGINIA: *Hardy Co.* Bass (LLW 509-10, 546) 2½ mi. N of Bass (LLW 408-10); Fabius (LLW 529, 532); Fisher (LLW 569); 2 mi. S Fisher (LLW 438); Kessel (LLW 434, 607, 805, 814-6); Lost City (LLW 156); 1 mi. NE Lost City (LLW 60-1; 1¼ mi. NE Lost City (LLW 145-6); 1½ mi. NE Lost City (LLW 100, 147); Lost River (LLW 65); Mathias (LLW 160-1, 204); Moorefield (LLW 262-5, 323, 325, 448-54, 459-61, 466-7, 480-8, 799, 801-3, 806-10); 2 mi. W Moorefield (LLW 570); 2 mi. NE Moorefield (LLW 591); 2 mi. SE Moorefield (LLW 23); 2½ mi. SE Moorefield (LLW 71); 3 mi. S Moorefield (LLW 276-8); 3.9 mi. SE Moorefield (LLW 227-32); 4 mi. S Moorefield (LLW 239-40); 4½ mi. N Moorefield (LLW 832); 7½ mi. SE Moorefield (LLW 475-9); Orndorff's Store (LLW 515-21); Purgittsville (LLW 400, 407); 2 mi. E Purgittsville (LLW 539); 3 mi. S Purgittsville (LLW 795, 804); 5 mi. SW Purgittsville (LLW 395-7); Rig (LLW 490, 522-4); 3 mi. SW Rig (LLW 608); 5 mi. SW Rig (LLW 411); 3 mi. N Rockoak (LLW 615-6); Scotts Ridge School (LLW 848); Wordensville (LLW 513). *Morgan Co.* 6 mi. S Berkeley Springs (LLW 655); 9 mi. E Berkeley Springs (LLW 658); 11 mi. E Berkeley Springs (LLW 733).

D. C.: Washington (USNM 46204-8).

Pseudacris nigrita feriarum-triseriata intergrades examined:

ARKANSAS: *Benton Co.* Siloam Sprgs. (OU 24151). *Greene Co.* Paragould (USNM 99688-91). *Jackson Co.* 11 mi. SW Newport (UIMNH 18450-62). *Lawrence Co.* (CNHM 21313-4, 8554; USNM 64873); Imboden (AMNH 44240, 22776-7, 22779-81, 22784-5). *Washington Co.* Fayetteville (USNM 118470-1).

ILLINOIS: *Clark Co.* Rocky Branch (INHS 1998). *Crawford Co.* Robinson (INHS 2801-2). *Jackson Co.* Grimsby (INHS 3338-9). *Perry Co.* Cutler (INHS 3340-1). *Richland Co.* Olney (CAS 2020-1, 2014; CNHM 38709-10; INHS 3750-91; UIMNH 3066-75). *Wabash Co.* 2.5 mi. N Allendale (INHS 4739-42). *Wayne Co.* Fairfield (CAS 10903).

INDIANA: *Allen Co.* Ft. Wayne (USNM 42679-81). *Bartholomew Co.* 2 mi. N Columbus (SAM 266). *Brown Co.* Brown Co. St. Pk. (INHS 4593-5). *Floyd Co.* Silver Hills (SAM 4 sp.). *Gibson Co.* ¾ mi. E Oakland City (SAM 7 sp.). *Greene Co.* Mineral Springs (CNHM 3033, 4096). *Hamilton Co.* 2 mi. SW Carmel (SAM 244). *Jackson Co.* 2 mi. S Tampico (SAM 5 sp.). *Marion Co.* Indianapolis (CNHM 21315-8). *Monroe Co.* 3 mi. N Bloomington (KU 20696-748); 4 mi. N Bloomington (AMNH 52560-2). *Morgan Co.* 2 mi. W Martinsville (SAM 249). *Owen Co.* Spencer (SAM 7 sp.). *Pike Co.* Pikeville (CNHM 2718). *Posey Co.* Mt. Vernon (AMNH 52502; INHS 3821-6); 4 mi. S New Harmony (INHS 3734-59; UIMNH 3086-95). *Vigo Co.* Terre Haute (CNHM 23446-9). *Wayne Co.* Fountain City (EC 1 sp.); Pennville (EC 1 sp.). *Wells Co.* Bluffton (CNHM 18092).

KENTUCKY: *Livingston Co.* 7 mi. E Paducah (INHS 4566-73). *McCracken Co.* 2 mi. E Paducah (UIMNH 13133-9).

OHIO: *Clermont Co.* (OS 621, 624, 1113). *Summit Co.* Kent (OS 1537 (2)).

OKLAHOMA: *Mayes Co.* 2 mi. W Locust Grove (OU 20557, 20559-60). *Seminole Co.* (OU 21909-11).

PSEUDACRIS NIGRITA TRISERIATA (Wied)

Hyla triseriata Wied, 1839, p. 249; Noble, 1923, p. 5. *Helocaetes triseriatus,* Baird, 1854, p. 60. *Chorophilus triseriatus,* Cope, 1889, pp. 342-347. *Chorophilus nigritus triseriatus,* Dickerson, 1908, pp. 157-160. *Pseudacris triseriatus,* Stejneger and Barbour, 1917, p. 31. *Pseudacris nigrita triseriata,* Wright and Wright, 1933, pp. 94-95.

Type locality.—Mt. Vernon, Posey Co., Indiana.

Range.—Northern and southern shores of Lake Ontario, west and southwest to extreme northern Texas and north to central Minnesota (see fig. 2).

Diagnosis.—A short legged chorus frog usually with five longitudinal stripes or pattern plainly derived from stripes; upper jaw with a light line narrowly margined below with dark; mid-dorsal stripe often forking posteriorly, occasionally broken up into a row of spots in which case the dorsolateral stripes are quite wide; usually a dark triangular mark between eyes; lateral stripes invariably present but seldom more pronounced than dorsals, contrary to the condition in the preceding subspecies; venter white, the breast often stippled with dark; ground color above gray, light brown, or greenish white with black, brown, or olive stripes; upper parts of limbs barred, spotted, or plain; dorsum smooth to uniformly granular, venter finely granular; tibia length from 41 to 47% of snout-vent length, averaging 42.6±.101; femora and feet likewise relatively shorter than in preceding subspecies; head length/body length ratio ranging from 25 to 35%, averaging 30.0%; head width/body length ratio from 25 to 34%, averaging 29%; eyes small and lateral in position, thereby giving the appearance of a wide interorbital space.

Comparisons.—Often specimens of this subspecies may be recognized at a glance by the small head which is strikingly narrower than the body. Un-

fortunately, this proportion difference cannot be measured because of the correlation of body width with such factors as gonad condition, humidity, and starvation. This race differs from *feriarum* by having the tibia usually less than 47%, ranging from 37% to 49% and averaging 42.5% of the body length, by the usual dorsal pattern of distinct longitudinal stripes, by the relatively smaller digital pads, and by the smaller head and eyes.

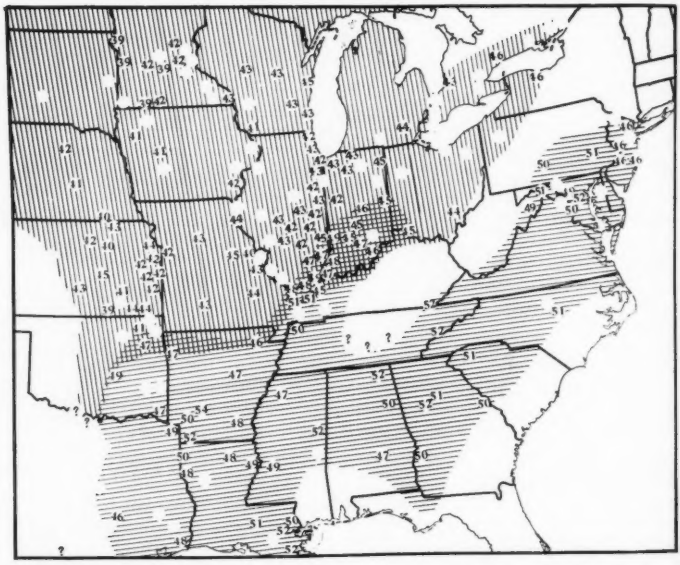


Fig. 2.—Range of *Pseudacris n. feriarum* (horizontal lines) and *Pseudacris n. triseriata* (vertical lines). Open circles represent localities from which specimens were examined; figures within symbols are T/B ratio means when two or more specimens were available from a locality.

Variation.—The absence of a north-south leg-length gradient within the subspecies may be seen by comparing ratio means for central Illinois and southern Wisconsin (fig. 2). The peripheral variation (length of legs) noted in *feriarum* is also seen in this subspecies, however, although it is less striking (table 2). The western New York and southeastern Ontario populations resemble *triseriata-feriarum* intergrades in body and limb proportions, possessing longer legs than do series from localities from northern Indiana westward. A similar tendency at the southwestern edge of the range could not be ascertained due to the paucity of material from north and central Texas. Moreover, although *triseriata* does appear to extend into northern Texas, it is in contact with *P. n. feriarum;* and intermediate populations must be considered intergrades.

Except in intergrading areas and the northeastern edge of the range, series of *triseriata* from any one locality are remarkably homogeneous (excluding rare aberrants). Similarly no other trends in geographic variation are evident. Series from one locality, however, may differ in varying degrees from a series in a nearby locality. Most pronounced example of this is the population in Cowley County, Kansas, which is comprised of short-legged frogs closely resembling series from Canada and the Rocky Mountains. The possibility of error in recording locality data seems remote in view of the fact that such specimens were examined from four different museum collections. Series from certain localities, notably in Missouri and Wisconsin, differ slightly from typical *triseriata* by the smaller head and by the depressed, truncate snouts.

TABLE 2.—Summary of variation in tibial lengths of *Pseudacris n. triseriata* expressed in percentages (exclusive of intergrading populations).

	Western N. Y.	Southern Ontario	Northern Illinois	Eastern Kansas
No. of specimens ..	25	33	126	43
Extremes	41–50	40–52	38–47	37–48
Mean	45.7	45.9	42.7	42.2

Intergrading populations of *triseriata* and *feriarum* are exceedingly variable and unpredictable. The extent of variation in large samples may include maxima for both subspecies and occasionally extremes not found in either. Rather than an accelerated transition from long to short legs within the intergrading area, the interbreeding populations are erratic in nature and sometimes exhibit the reverse. A series of 48 intergrades from Richland County, Illinois (only 25 miles south of consistently typical *triseriata*) averages 47.3% in tibial length, whereas a series of 36 specimens from New Harmony, Indiana (50 miles south of the above locality) averages 46.3% (fig. 1). Twenty-five Monroe County, Indiana, specimens display *feriarum* characters and average 47.0% but 19 Livingston County, Kentucky (150 miles to the south) are intermediate in pattern and average 45.5%. The chaotic nature of these intergrading populations is probably an important factor in the confusion which has involved the two races.

The marked variability and erratic nature of the intergrading series and the relativity narrow geographic contact between *triseriata* and *feriarum* suggest the secondary intergradation of Mayr (1942, p. 99). If these phenomena actually do demonstrate hybridization as opposed to primary intergradation, it appears that the present contact between the *verrucosa-nigrita-feriarum* group and the *septentrionalis-triseriata* group, via *feriarum-triseriata*, has been recently reestablished.

The smaller ratio means of central Minnesota, Nebraska, and Dakota populations (fig. 2) are probably intergrades with the northern *septentrionalis*, but redefinition of this subspecies is outside the scope of the present report.

Remarks.—The type locality of this subspecies actually is located in an intergrading zone between this and the preceding subspecies. This is extremely unfortunate and leaves some question as to which form Prince Wied described. His description is rather inadequate and might fit either race. The character of the dorsolateral stripes (". . . *Unter jeder Seitenreihe der Rückenflecken und über dem von der Nase kommenden Seitenstreifen steht eine Reihe kleiner runder Fleckchen*" . . .) and the length of the limbs (". . . *Länge 1″ ½″; Länge mit ausgestreckten Hinterbeinen, 2″ 9″.*") actually suggest *feriarum* more than *triseriata*. Moreover, six topotypes collected by us are intergrades but show closer affinities to *feriarum* (Plate 1). In view of this, synonymizing *feriarum* under the earlier name of *triseriata* and renaming the mid-western race has been seriously considered.

The exact spot visited by Wied, however, could not be determined from his narrative. Since he traveled by boat the type specimen, presumably, was collected in the Ohio River bottom-lands. In an intergrading area and especially in the case of these forms, this fact might be of considerable significance. It also seems unwise to synonymize the name *feriarum* with a series of only six topotypes available for examination. Furthermore, a much more adequate sample (36 specimens) was obtained four miles south of New Harmony (still in Posey County but out of the river valley) and this consists of definite intergrades which do approach *triseriata* more closely than *feriarum* in the character of leg length and dorsal pattern.

It thus seems advisable to accept Mt. Vernon, Indiana, as the type locality for the more western race, but the possibility that a large series from Mt. Vernon (or the Ohio River bottoms nearby), may average closer to *feriarum* must be considered. If the type of habitat is actually significant (*feriarum* largely restricted to bottom lands), *triseriata* would supersede *feriarum* and a new name would need be proposed for the western population. The confusion in the literature which would result from such a change is obvious. Influenced by this consideration, we suggest continuing the use of the name *triseriata* for the western population of relatively short leg-length.

The range of the subspecies, as here defined, is much more restricted than formerly believed. The absence of the species from the Laurentian Shield has been noted (Wright & Wright, 1949), and Dr. E. B. S. Logier informs us (*in litt.*) that the ranges of the Ontario forms do not meet anywhere in the province. The replacement of the species by *P. brachyphona* in southwestern Pennsylvania, western West Virginia, central Kentucky, and possibly central Tennessee has been mentioned. Similarly in Kansas, Oklahoma, and Texas *P. n. triseriata* is replaced by another species, *Pseudacris clarkii*. A single record (BUM 0744) from Helotes, Bexar Co., Texas, is considerably west of the other records of *P. nigrita*. That this specimen has been confused with *P. clarkii*, which is known to occur in that part of Texas, is unlikely because of the longer legs of the latter species. That it may be an error in cataloging, however, is possible. Too few specimens were available from Ohio, western Pennsylvania, western Virginia, and western West Virginia, as well as in north central Texas, to indicate the nature of these populations. Additional series from these areas may shed some light on the

peripheral variation exhibited by both races in the northeast. The area of intergradation in southwestern Ohio as indicated on fig. 2 is subject to revision inasmuch as Walker (1946, pp. 51-56) did not note a leg length gradient within the state.

Pseudacris nigrita triseriata examined:

ILLINOIS: *Adams Co.* Quincy (INHS 2678-8). *Bond Co.* Reno (UIMNH 790-1). *Brown Co.* 2 mi. W Meredosia (INHS 4687-702). *Champaign Co.* Fisher (INHS 2799-800, 2806-8, 3132-3, 2607; UIMNH 766, 769); Seymour (INHS 2202); St. Joseph (INHS 2360); Urbana (UIMNH 782-5, 787-9). *Christian Co.* 5 mi. S Taylorville (UIMNH 786). *Coles Co.* Charleston (INHS 3929-33, 1908-9); Fox Ridge State Park (INHS 1821); 7 mi. S Mattoon (INHS 3816-9, 3830-2). *Cook Co.* Chicago (CNHM 48975-6); Homewood (CNHM 42600); Lemont (CAS 1003, 1009, 1011, 1013-4); Riverside Woods (CAS 1879, 1881, 1883-5, 1887, 1890-1, 1893). *Cumberland Co.* Greenup (INHS 2809-15; CNHM 37890); Neoga (INHS 3833-7). *Douglas Co.* Chesterville (INHS 2847, 2850-1). *Du Page Co.* Naperville (CNHM 38712-3, 38716-9). *Ford Co.* Paxton (INHS 1814-5). *Hancock Co.* Hamilton (INHS 2671). *Iroquois Co.* 1 mi. N Cissna Park (INHS 5583). *Jasper Co.* Newton (INHS 3792-813; UIMNH 3076-85). *Kankakee Co.* Hopkins Park (CAS 4708-9, 4711-3, 4715-9, 4723). *Lake Co.* Cary (INHS 2205); Deerfield (CAS 419, 424-5, 430, 417, 450, 452, 458, 462-3, 465, 468-9, 471, 474, 476, 480, 484, 486, 488, 492, 498, 966, 998-9, 1930-2, 1935-6, 1938, 1940, 1942-3, 1947, 1956-7, 1960). *McLean Co.* Normal (MCZ 2052). *Monroe Co.* Burksville (INHS 2274). *Montgomery Co.* 7 mi. N Litchfield (CAS 1091). *Morgan Co.* 3 mi. E Chapin (INHS 4598-610); Meredosia (CNHM 3267). *Piatt Co.* Monticello (INHS 241-4). *Randolph Co.* 3 mi. N Chester (INHS 5016-7); 5 mi. N Chester (INHS 5341). *Rock Island Co.* Rock Island (INHS 5250); Moline (INHS 4441). *Sangamon Co.* Springfield (CNHM 23463-4). *Shelby Co.* 1½ mi. W Windsor (INHS 4617-36). *Vermilion Co.* Muncie (UIMNH 776-80); Danville (UIMNH 771, 773).

INDIANA: *Cass Co.* Peabody Woods (CNHM 18093). *Kosciusko Co.* 1½ mi. S North Webster (SAM 1075). *Lake Co.* Hammond (CNHM 5933); Miller (CNHM 2845). *La Porte Co.* Smith (CNHM 30560-1, 41089). *Marshall Co.* Lake Maxinkuckee (USNM 42677-8). *Noble Co.* 2 mi. NE Wilmot (SAM 1293 (3)). *Porter Co.* Dune Acres (CNHM 23501-3, 23460-2, 23476); Tremont (CNHM 13197, 30610). *Tippecanoe Co.* 2 mi. NE Lafayette (SAM 5 sp.). *Tippecanoe-Clinton Co. line.* 1 mi. W Fickle (SAM 6 sp.). *St. Joseph Co.* South Bend (SAM 6 sp.). *Wabash Co.* 1½ mi. NE Urbana (SAM 8 sp.).

KANSAS: *Anderson Co.* 5 mi. N Garnett (KU 7273). *Bourbon Co.* Ft. Scott (KU 24225); Fulton (KU 34302). *Cloud Co.* W Miltonvale (KU 17261-7). *Cowley Co.* Udumfield (CNHM 18539); Winfield (MCZ 19380; CNHM 28481; USNM 90284); 7 mi. NE Winfield (KU 17595-5); 2 mi. SE Winfield (KU 20348-9). *Douglas Co.* 3 mi. NW Lawrence (UIMNH 15445-51). *Montgomery Co.* 5 mi. N Cherryvale (AMNH 32475-9). *Osage Co.* 1 mi. N Carbondale (KU 17620-9). *Reno Co.* Medora (CNHM 18091). *Riley Co.* Manhattan (CNHM 18081-2).

MICHIGAN: *Branch Co.* 8 mi. N Quincy (USNM 108547). *Washtenaw Co.* (KU 13636-8); Ann Arbor (MCZ 4157-68).

MINNESOTA: *Anoka Co.* Blaine Twp. (UM 92, 105); Bunken Lake (UM 277). *Carleton Co.* Moose Lake Region (UM 977-8). *Chisago Co.* (UM 942-3). *Faribault Co.* 3 mi. E Blue Earth (UM 890, 885-7). *Fillmore Co.* Forrestville (UM 1662). *Houston Co.* (UM 102, 966); S La Crescent (UM 1488); Reno (UM 896). *Hennepin Co.* Ft. Snelling (UM 65); Minneapolis (UM 106); Lake Minnetonka (UM 278-9. *Isanti Co.* Cedar Creek Bog (UM 925). *Jackson Co.* Heron Lake (UM 121-5); Little Sioux (UM 1 sp.); Round Lake (UM 894). *Kandiyohi Co.* Nest Lake (UM 1073); Willmar (UM 112). *Lac Qui Parle Co.* Lac Qui Parle (UM 992-5). *Martin Co.* East Chain (UM 888-9). *Meeker Co.* Dassel (UM 1494). *McLeod Co.* Eagle

Lake (UM 997-1002). *Mille Lacs Co.* (UM 225, 855). *Olmstead Co.* 4 mi. N Rochester (UM 922). *Ramsey Co.* (UM 67-9). *Rock Co.* NW Hardwick (UM 1107). *Scott Co.* Savage (UM 37). *Washington Co.* Stillwater (UM 89).

MISSOURI: *Chariton Co.* Sumner (CAS 8783). *Jackson Co.* (CNHM 11878-9; USNM 58077-81); Blue Springs (AMNH 52506-7); Warrensburg (KU 8070-1); Westport (KU 8067-9). *Iron Co.* Ironton (UIMNH 16371). *Jefferson Co.* (USNM 37044). *Lincoln Co.* (USNM 58075-6). *Madison Co.* (USNM 58070). *Montgomery Co.* (USNM 58072-4). *St. Charles Co.* (USNM 58071). *St. Louis Co.* St. Louis (MCZ 2283; USNM 18018-1, 14550, 58067-9). *Webster Co.* 2 mi. W Fordland (USNM 85585-6).

NEBRASKA: *Holt Co.* (USNM 82048-64); Atkinson (CNHM 11374-6). *Jefferson Co.* Thompson (USNM 90799-806). *Merrick Co.* Central City (USNM 118419-27).

NEW YORK: *Monroe Co.* West Henrietta (UR 2486-7, 899, 2547, 2490-1); Rochester (UR 4441, 1435, 4180, 2034, 6528); Parma (UR 901, 2235-41); Parma-Ogden (UR 2233); Parma-Hilton (UR 838, 100); West Webster (UR 3427); Burritt Road (UR 3135).

OHIO: *Lorain Co.* (CAS 5976). *Champaign Co.* Urbana (EC 1 sp.).

OKLAHOMA: *Craig Co.* ½ mi. S Junct. 66 & 69 (OU 23728). *Nowata Co.* Delaware (USNM 94242-3); *Roger Co.* Talala (USNM 94248-51). *Tulsa Co.* 7 mi. NE Tulsa (OU 23228).

ONTARIO: *Bruce Co.* Lucknow (ROM 1773). *Frontenac Co.* (ROM 4830, 3456); Arden (ROM 3365, 3860); Eagle Lake (ROM 7027, 4827-9, 4831). *Gray Co.* Cape Rich (ROM 1404-5). *Kent Co.* Lake St. Clair (ROM 2197). *Lambton Co.* Thedford (ROM 5224). *Leeds Co.* Gananague (ROM 6819). *Petersboro Co.* Oak Lake (ROM 52). *Simcoe Co.* Tossorontia (ROM 5975-6). *Waterloo Co.* Galt (ROM 751). *York Co.* Leaside (ROM 4832-8, 4840); Toronto (ROM 6879-80, 1403, 4731, 5030); Wilcox Lake (ROM 4725).

PENNSYLVANIA: *Venango Co.* (UIMNH 16682).

SOUTH DAKOTA: *Brookings Co.* 10 mi. S Brookings (AMNH 52501). *Lyman Co.* Reliance (AMNH 32422).

WISCONSIN: *Burnett Co.* Webster (CNHM 21694). *Chippewa Co.* Stanley (AMNH 5380). *Clark Co.* Dorchester (HKS 1200); Hewitt Twp. (CNHM 13031); Dewhurst Twp. (CNHM 14621-32); Worden Twp. (CNHM 5524-5, 12653, 5526). *Dodge Co.* Beaver Dam (UIMNH 1452-71). *Manitowoc Co.* Two Rivers (HKS 1016). *Milwaukee Co.* Wauwatosa (MPM 1348-9, 1354-7, 1260). *Richland Co.* (INHS 4464). *Waupaca Co.* Lawrence Twp. (CNHM 14735); Waupaca (HKS 1276).

ZOOGEOGRAPHIC CONSIDERATIONS

The phenomenon of peripheral variation and the erratic nature of the intergrading populations may be of some significance to the understanding of the phylogeny of the group. We feel that the range of a *feriarum*-like ancestor, formerly widespread over eastern United States, may have been bisected by an eastward extension of prairie, which subsequently provided an avenue for invasions of *triseriata*. In the east a hiatus in the range, occupied by another species *P. brachyphona*, prevents intergradation. The peripheral variants, rather than being intergrades, thus appear to be intermediate because their characters are being swamped through interbreeding with adjacent typical populations.

This explanation does not account for the variation in the southwestern populations but it is possible the range of *triseriata* may actually extend far-

ther south in Texas than is indicated by the rather scanty records and intergrade with *feriarum* along the eastern edge of the Great Plains. Factors limiting the range of the species in the southwest are likewise unknown, but the replacement of *P. nigrita* by *P. clarkii* suggests competition.

REFERENCES

BAIRD, S. F. 1854—Descriptions of new genera and species of North American frogs. Proc. Acad. Nat. Sci. Philadelphia 7: 59-62.

BRAGG, A. N. 1948—Observations on the life-history of *Pseudacris triseriata* (Wied) in Oklahoma. Wasmann Collector 7(4): 149-168.

BURT, C. E. 1938—The frogs and toads of the southeastern United States. Trans. Kansas Acad. Sci. 41: 331-360.

CAGLE, F. R. 1942—Herpetological fauna of Jackson and Union Counties, Illinois. Amer. Midl. Nat. 28(1): 164-200, figs. 1-15.

CARR, A. F. 1945—A contribution to the herpetology of Florida. Univ. Florida Biol. Series 3: 1-118.

CONANT, R. 1945—An annotated check-list of the amphibians and reptiles of the Del-Mar-Va Peninsula. Soc. Nat. Hist. of Delaware, Wilmington: 1-8, 1 map.

———1947—Reptiles and amphibians in Delaware: 23-25. *in* Delaware, a history of the first state. Lewis Historical Publ. Co., New York.

COPE, E. D. 1862—On some new and little known Anura. Proc. Acad. Nat. Sci. Philadelphia 14: 151-159.

———1875—Check-list of North American batrachia and reptilia with a systematic list of the higher groups and an essay on geographical distribution based on specimens contained in the United States National Museum. Bull. U. S. Nat. Mus. no. 1: 1-104.

———1889—The batrachia of North America. Bull. U. S. Nat. Mus. no. 34: 1-525, pls. 1-86, figs. 1-120.

DICKERSON, M. C. 1908—The frog book. Doubleday, Page and Co., New York, x+253 pp., 94 pls.

MAYR, E. 1942—Systematics and the origin of species. Columbia Univ. Press, New York, vii+334 pp., 29 figs.

NEILL, W. T. 1949—The status of Baird's chorus frog. Copeia, no. 3: 227-228.

NOBLE, G. K. 1923—The generic and genetic relations of *Pseudacris*, the swamp tree frog. Amer. Mus. Nov. no. 70: 1-6, figs. 1-4.

SCHMIDT, K. P. 1938—A geographic variation gradient in frogs. Zool. Series of Field Mus. Nat. Hist. 20(29): 377-382.

SMITH, H. M. 1947—*Pseudacris clarkii* and *P. n. triseriata* in Texas. Herp. 3, pt. 5: 183-184.

STEJNEGER, L. AND T. BARBOUR 1917—A check-list of North American amphibians and reptiles. Harvard Univ. Press, Cambridge, i+120 pp.

———1933—*Op. cit.* 3rd Edition.

TAYLOR, E. H. 1935—Arkansas amphibians and reptiles in the Kansas University Museum. Univ. Kansas Sci. Bull. 22(10): 207-218.

WALKER, C. F. 1946—The amphibians of Ohio. Part I. The frogs and toads. Ohio State Mus. Sci. Bull. 1(3): 7-109, pls. 1-14.

WIED, M. PRINZ ZU 1839—Reise in das Innere Nord-Amerika in den Jahren 1832-1834 bei J. Hoelscher. Coblenz, vol. 1 (Chapter IX. Reise von New-Harmony nach St. Louis am Mississippi und Aufenthalt daselbst, von 16, März bis 9, April, 1833, pp. 215-251).

WRIGHT, A. H. AND A. A. WRIGHT 1933—Handbook of frogs and toads. Comstock Publ. Co., Inc., Ithaca, ii+231 pp., 81 pls.

———1949—Handbook of frogs and toads of the United States and Canada. Comstock Publ. Co., Inc., Ithaca, iv+640 pp., 126 pls., 37 maps.

PLATE 1.—Top row: *P. n. feriarum* (INHS 4165-70, Huntington County, Pennsylvania). Second row: *P. n. feriarum* (INHS 5614-7, Johnson County, Illinois). Third row: *P. n. triseriata* (INHS 3821-4, Posey County, Indiana). Bottom row: *P. n. triseriata* (INHS 4682-5, Morgan County, Illinois).

Evidence for Olfactory Discrimination by the Bobwhite Quail

Hubert Frings and William A. Boyd

The Pennsylvania State College, State College, Pa.

Little work has been done on the sense of smell of birds, and it is generally believed that this sense is poorly developed (Warden et al., 1936; Prosser, 1950). Hamrum (1949), studying the chemical senses of the bobwhite quail, attempted to train the birds to associate the odor of coumarin with food. He had little success in this, however, since coumarin quite unexpectedly proved to be repellent to the quail. This finding led us to try to determine what odors would attract or repel quail. The primary purpose of this experiment was not achieved, however, because of the interesting and interfering side-results which are described here.

Materials and methods.—Fifteen adult bobwhite quail, *Colinus virginianus virginianus,* were divided into 5 groups of 3 birds each. Each group was housed in a wire cage, 12 x 12 x 24 in., with mesh floors so that feces could fall through onto paper placed beneath. The birds were fed scratch grain placed in two similar metal feeders at opposite sides of the cage. These feeders were marked on the back for identification purposes with a small letter "A" or "B"; otherwise they were as similar as possible. To minimize loss of food through scratching by the birds, each feeder was covered with a ⅛ in. wire mesh. Drinking water was available at all times. The cages were placed in a screened open-air insectary; thus the quail were under natural outdoor spring and early summer conditions.

The original object of this study was to induce the quail to take equally from the two feeders regardless of the positions of the feeders in the cage. The feeders were interchanged in position irregularly, as determined by a coin-toss each day, so that any position habits could be discovered. Once the birds were taking equally from both containers, we planned to place some odorous material on one of the feeders and thus to discover its possible effect on feeding. The amount of food taken from each of the feeders was determnied by daily weighings.

Observations and interpretations.—In the early stages of the experiment the birds developed some position habits in feeding, but these were readily given up. As the days succeeded each other, however, the quail in four of the five cages began to feed from one feeder preferentially over the other, regardless of the position of the feeder in the cage. This was shown by the birds' taking

1 We wish to thank Mr. Roger Latham and the Pennsylvania Game Commission for supplying the quail and the cages used in these experiments. Authorized for publication on December 11, 1950 as paper No. 1641 in the journal series of the Pennsylvania Agricultural Experiment Station.

more than 85% of their food from one feeder. In two of the cages they fed from the preferred feeder almost 100%. In Cages I, IV and V the birds fed preferentially—in Cage I almost exclusively—from the feeder labeled "B". In Cage III the birds fed almost exclusively from the feeder labeled "A". The quail in Cage II showed less clear-cut preferences, taking for a short time from one feeder and after that shifting for a time. It should be emphasized that these feeders were alike except for the letters on the backs, so far as we could determine, and that they were shifted irregularly to eliminate the possibility of position habits in feeding.

At this point the object of the experiment was changed. Since the birds in each cage obviously preferred one feeder over the other, they must have been able to discriminate between the feeders through some sensory cues. The objective now became to find the nature of these cues.

It seems highly improbable that hearing could be used for discrimination in this case, since the feeders were made of the same material. Taste and touch would also seem to be eliminated from consideration, because there was no evidence of tactile or gustatory exploration of the feeders by the birds; the reaction was obviously one at a distance. The two most likely possibilities, therefore, were sight and smell.

The first assumption would be that the birds were using visual cues. To test this the feeders from Cages I and III were interchanged. If the birds associated the letters on the feeders with food, they should have fed after the interchange from the feeder with the same letter as that from which they had been feeding. However, the preferences in the cages immediately shifted, so far as the letters were concerned, the birds in Cage I taking from feeder "A" and those in Cage III taking from feeder "B." Thus the birds changed letters, but followed the preference of the birds in the cage in which the feeder had previously been. This eliminated the possibility that the birds associated the letter on the feeder with food. It further eliminated the possibility that the quail associated other stray marks on the feeders with food, since in this case no association could be present immediately following the shift. In Cages IV and V both feeders were covered with cloth, thus completely changing the appearance. The birds still fed from the feeder from which they had been feeding. This was also later done with the feeders in Cages I and III without shifting the preference. These experiments would thus seem to eliminate the sense of sight.

It follows, therefore, that the sense of smell, or some unknown sense, must be involved in the differentiation. To test the olfactory hypothesis, the feeders were variously interchanged from cage to cage. Feeders from Cages IV and V, in both of which the birds were taking from the one marked "B," were interchanged without affecting the preference. Apparently the birds followed the preference of those in the other cage. Feeders from Cages I and III were similarly interchanged with the results noted above, the birds in each cage following the preference of those in the other cage. The shifting of feeders was repeated three times always with the same result. It is interesting

to note that the birds, while following the preference of the birds in the cage from which the feeders came, seemed to notice the shift in feeders, for they fed very lightly for a day or two following the shift. On these days there was also a tendency to take a little more from the non-preferred feeder, up to 30%.

A further test of the olfactory hypothesis was made by interchanging feeders "III A" and "I A" in Cages I and III. This gave the birds in Cage I feeders "III A" and "I B," both preferred over their mates, and the quail in Cage III feeders "I B" and "III A," both non-preferred. The quail in Cage I, with the two preferred feeders, fed as usual from the feeder preferred before the exchange and took the normal amount of food. The birds in Cage III, with the non-preferred feeders, fed lightly and about evenly from both. In Cage I, the birds continued to feed from the originally preferred feeder, while in Cage III the birds soon developed a new preference for the "A" feeder. Thus essentially the original situation was restored, with the birds in Cage III taking from "A" and in Cage I from "B." The feeders were thereupon interchanged, with the result that the quail in Cage I took from "A" while those in Cage III took from "B." Thus the birds in Cage III ignored the feeder they had preferred earlier ("A") for the feeder which the quail in Cage I had been taking from immediately before the shift. Those in Cage I now took from the feeder which had been earlier non-preferred ("A"), but which was recently preferred by the birds in Cage III.

It would thus seem clear that the birds were differentiating between the feeders by the sense of smell. Further, the odor on the feeders apparently was a species odor, since the preference of birds in one cage was carried over to another. But the odor also seemed to have some individual variation, for the birds could distinguish a feeder from which they had been feeding from a feeder preferred by birds in another cage. It would seem moreover that the odor material is rather volatile, as indicated by the last experiment, since the birds in Cage III fed from the feeder recently preferred by the quail in Cage I rather than from the feeder they had used a few days previously.

All attempts on our part to distinguish between the feeders by odor failed. Either the odor is one which is indistinguishable to man or the quail has a more acute sense of smell than man. Either one of these implies a fairly acute sense of smell on the part of the birds, possibly a more acute sense of smell than is found in man.

An obvious possibility as the substance which enabled the quail to distinguish one feeder from the other would be the secretion of the uropygial gland. The birds take this substance onto the beak and spread it over the feathers, and it might thus get onto the feeders during feeding. To test this, some of the oil was extracted from the glands of the birds in each cage and was applied to the non-preferred feeder in each case. There was no effect whatsoever upon the preference. It thus seems unlikely that this is the odor substance involved.

If it is assumed that the skin of the quail produces oils which give it a characteristic species odor, as does the skin of the mammal, then it is easy

to see how the quail would develop a preference for one feeder over the other. As they fed they would accidently feed more from one than from the other, and by brushing against the feeder would transfer the odor to it until it was clearly marked. Whenever reversals in feeding preferences occurred, it was noted that the birds had fed lightly for a few days previously. If the odor substance is assumed to be rather volatile and never applied heavily to the feeders, as suggested by the results of the trials with the two preferred feeders in one cage, it is easy to see how this could occur.

It would seem, therefore, that the quail has a more highly developed sense of smell than is generally assumed. The usual belief is that visual and tactile cues are most active in the feeding behavior of birds. The results of our experiment, and those of Hamrum (1949), show that future students of these behavior patterns in quail—and possibly in other birds as well—should assume that olfaction may be active unless they prove it to be non-active.

Summary.—Caged bobwhite quail learned to discriminate between two feeders which to man were apparently the same. Changes in the appearance of the feeders did not affect the discrimination. Interchanging the feeders between cages of quail showed that the olfactory sense was probably involved. The differentiating odor substance was not determined, but it is suggested that it is in the nature of a species odor transferred to objects as the quail touches them. Since the odor was undetectable to man, the quail probably has a rather well developed sense of smell.

REFERENCES

HAMRUM, C. L. 1949—Experiments on the senses of taste and smell in the Bobwhite quail (Colinus virginianus virginianus). Thesis, M.S., Penna. State College.

PROSSER, C. L., ed. 1950—Comparative animal physiology. Phila., W. S. Saunders Co.

WARDEN, C. J., T. N. JENKINS AND L. H. WARNER 1936—Comparative psychology. Vol. III. Vertebrates. New York, Ronald Press.

Columbian Sharp-tailed Grouse (Pedioecetes phasianellus columbianus) in the State of Washington

Charles F. Yocom

State College of Washington, Pullman

This western race of the sharp-tailed grouse (*Pedioecetes phasianellus columbianus*) formerly inhabited the lowlands of the Great Basin from the Rocky Mountains to the Cascades and the Sierra Nevada. This grouse was discovered in 1805 by Lewis and Clark on the bunchgrass and sagebrush plains of the Columbia River and was named by Ord in 1815 (Bent, 1932).

According to reports of early pioneers who settled in eastern Washington, the Columbian sharp-tailed grouse (*prairie chicken* to them) was the most abundant and best known game bird. These grouse inhabited the prairies which extended over most of the Columbia Plateau of eastern Washington. They were common also on the areas where forests met the prairies. Winter months found sharptails concentrated along the creek bottoms and draws where such trees and shrubs as *Alnus, Betula, Amelanchier, Crataegus, Rosa,*

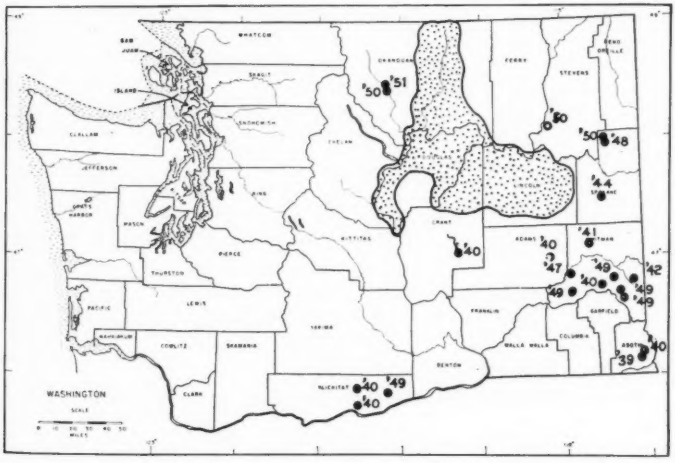


Fig. 1.—Present range of the Sharp-tailed Grouse in the State of Washington. The dots represent isolated records and the year indicates when they were last recorded in these localities.

Symphoricarpos, and *Salix* grew in abundance. It was in such places that homesteaders in winter months killed all the birds they could carry home. I have been told that boys often killed these grouse with stones and sticks. Hunters with 22 rifles could shoot an entire flock perched in a tree without causing a bird to flush. Later when shotguns were used more often the sharptails were heavily persecuted because of their straight flight and their characteristic of flushing singly. This was common knowledge among the hunters who shot these birds only 35 to 40 years ago.

DECLINE OF THE SHARPTAIL

Early pioneers who arrived in the late sixties and seventies passed through the prairies and settled in the wooded areas such as the Ponderosa Pine Belt of Spokane and Lincoln counties. These areas were chosen first for settlement because wood and fresh water were available. Marsh areas were drained and Ponderosa Pine timber was cut and replaced by fields and pasture (Bernard, 1947). Temporarily this may have benefited the sharptails by retarding plant succession and thus creating suitable habitat and food for them. Later more settlers located along the few rivers and streams in the Columbia Plateau. Gradually the plows turned under the rich prairie lands. By 1900 hundreds of homesteads were established throughout the Palouse Hills, Big Bend, and in the valleys of the Okanogan Highlands. Sharptails apparently were very abundant in the early stages of settlement, but their numbers were soon to decrease sharply.

Accounts of the Rapid Decrease of Sharptails.—William Hegler of St. John, Washington, who was formerly a County Game Commissioner, told the author that *prairie chickens* were very numerous about 1908 in the vicinity of Cherry Creek along the western edge of Whitman County, but decreased very rapidly about 1912 to 1914 when the area became intensively cultivated. He stated, "The birds were killed very easily; whenever ranchers went out they were able, in a short time, to kill all they could carry home."

Another account is as follows (Yocom, 1943): "Mr. L. E. Hall, a retired Palouse farmer, told the author that sharp-tailed grouse afforded good hunting until about 1914. The birds resorted to nesting in unburnt stubble fields after the depletion of native cover. The farmers started burning their stubble with the coming of the caterpillar tractors. Mr. Hall recalls destroying many sharp-tailed grouse nests when he burnt 150 acres of stubble during the spring of 1915. After the stubble had burnt, 16 sharp-tailed grouse nests were found, each containing from 15 to 18 eggs. That was the last year he recalls having seen many of these birds."

Other accounts from eastern Washington indicate that sharptails decreased at about this time.

As the bunchgrass was replaced by cultivated fields and brushy draws and creek bottoms replaced by grubbed out ditches and gullies, the "space requirement" for this bird apparently could not be met. The elimination of their native habitat (bunchgrass and brushy draws and creek banks) beyond a

certain point accounts for their disappearance from most of their former range.

The caterpillar tractor, by causing a radical change in farming, hastened the final eviction of this grouse from its former range. Ranching on a large scale became possible and as a result land holdings under one ownership grew by leaps and bounds from the "80 or 160 acres" of the "homestead era" to over 530 acres per farm in Whitman County in 1940 (Yocom, 1943).

Field borders formerly used as travel lanes for horse-drawn machinery were plowed under, fence rows eliminated, and horse pastures plowed and put into grain production because they were no longer needed. Apparntly, sharptails were able to nest successfully in stubble fields until burning became a common practice to eliminate heavy stubble which would clog up large gang plows pulled by caterpillars.

The picture just presented, though simple, is tragic. A fine game bird was eliminated from its former vast prairies and brushy draws by an economic change from grazing to intensive farming.

PRESENT STATUS

The geological structure of eastern Washington is in part one of the reasons why sharp-tailed grouse can still be found in the State. The Columbia Plateau includes all of southeastren Washington (roughly 12,000 square miles) with the exception of the Blue Mountains. Underlying the entire area are consecutive layers of basalt. The Spokane and Columbia rivers skirt the northern edge of this Plateau for more than a hundred miles, but they receive only one-third of the drainage; the remaining two-thirds drains into the Snake and the Columia along the southwestern margin (Bretz, 1928). The region is dissected generally in a northeast-southwest direction by many channeled scablands. These elongated tracts of almost bare basalt are cut into a maze of buttes and canyons, bordered by rocky lands now used as cattle range. Many potholes and lakes are scattered throughout these channels. It is in some of this scabland which defies man's plows and caterpillars where sharptails are to be found today.

At present the largest concentration of Columbian sharp-tailed grouse are in Lincoln, Grant, Douglas, and Okanogan counties. This represents a large territory from near the international boundary of Canada and the United States at Oroville, Washington, on the Okanogan River; southwesterly along the breaks of the Columbia River to Waterville, Douglas County; east along Crab Creek, Lincoln County, to the vicinity of Harrington; thence to the breaks of the Spokane and Columbia rivers in Lincoln County. This vast area is not a continuous range for this species. Actually the population centers are quite scattered.

RECENT RECORDS OF SHARP-TAILED GROUSE BY COUNTIES

Since 1940 the writer has been collecting information on sharp-tailed grouse in Eastern Washington. Much of the remaining habitat for this species is restricted to the channeled scablands which also support the main

breeding areas of waterfowl and along the grassland-breaks of the rivers. Waterfowl surveys conducted in these uncultivated lands have afforded excellent opportunities to obtain records on sharptails. Much information was collected by talking to ranchers and other people working in the areas.

The writer is greatly indebted to ranchers, game department personnel, sportsmen, students and other people for many of the following records. The authority or source follows each record unless it is that of the writer's. Locations of some of the recent records and the present range of sharp-tailed grouse are indicated on the map (fig. 1).

Fig. 2.—Sharp-tailed Grouse habitat northeast of Delrio in northern Douglas County. In addition to Sharp-tailed Grouse this glaciated scabland supports waterfowl, Hungarian Partridges, Ring-necked Pheasants and Sage Grouse.

Asotin County.—A brood of seven 4 miles south of Anatone, 1939 (E. A. & F. M. Hendrickson); two seen by same parties on breaks of Snake River east of Anatone, 1938; four seen near Anatone, 1936 (David Barslev); a few sharp-tailed grouse were known to have been on the Albert Kiesecher ranch 5 miles east of Anatone, 1940. Undoubtedly, this species still persists in limited numbers along the breaks of the Snake River in Asotin County.

Whitman County.—Two seen by H. L. Eastlick a few miles northeast of Pullman, April 19, 1941; three seen by same party at south end of Rock Lake, middle of August, 1941 (Yocom, 1943). A few birds were known to have persisted in the bunchgrass-covered breaks of the Snake River north of Almota to as late as 1941. There were 17 observed in one flock in 1939 (Jos. Drolet). Five grouse (apparently sharp-tailed grouse according to the description) were seen several times during the summer around the farm lots and orchard of the Roy Held Ranch, Whelan Area northeast of Pullman, 1942 (Roy Held). One was seen in the orchard of the Wiedrich Ranch, one-half mile south of confluence of Rock Creek and Palouse River, fall, 1947. This is the first sharp-tailed grouse that had been observed in this area for several years. Mr. S. Wiedrich homesteaded here in 1902. Formerly sharp-tailed grouse were abundant in this area (Fay Wiedrich).

A flock of 10 birds was seen in high grassy and weedy area on ridge between Almota Creek and Little Almota Creek, 1500 ft. elevation, 1¾ miles east-south-east of Almota, Section 17, T14N, R43E, March 6, 1949 (Earl J. Larrison, letter). One flushed from breaks of Snake River Canyon, near Wawawai, April 23 and two flushed April 30, in the same general area. On May 20, two were flushed from the same location; these were believed to have been the same pair flushed previously, 1949 (D. D. Earp and A. G. Canaris). Approximately 25 were seen by A. Brenner on the J. Miller ranch (T15N, R43E, Sec. 27) on the northeast of Almota, fall, 1949 (Eugene Dziedzic). A few sharptails are known to be in the vicinity of Hay at the present time.

Adams County.—Sharp-tailed grouse continued to persist in the rangeland south of Twelve-mile Slough until about 1940. This area is 4 miles northeast of Benge. Formerly grouse were abundant in the Drumheller Channel of western Adams County; no recent records are available.

Spokane County.—Formerly abundant in southern part of county. Approximately 75 known to have been in the vicinity of Turnbull Slough in 1933. These disappeared but three were seen on the Turnbull National Wildlife Refuge in the fall of 1944 (Bernard, 1947). Recent records for the northwest corner of the county are: Six were observed one mile north and one and one-half miles east of the Deer Park airport in logged-over country in 1946. The birds were approximately one mile from farm land (Larry Wadkins). Twenty-five or thirty were seen in the same general area in the fall of 1947 (W. W. Wadkins); a few were seen in 1948 (E. J. Robins); and a small flock was known to be in that same area in 1950 (Stanley Gunther).

Fig. 3.—A side canyon along the Snake River which formerly was an important wintering area for Sharp-tailed Grouse; now only an occasional bird is seen. Note the thickets of deciduous trees and shrubs (*Populus tremuloides, Philadelphus lewisii, Physocarpus malvaceus, Crataegus* sp., *Symphoricarpos* sp.) in the main canyon and side draws.

Stevens County.—Recent reports of farmers who live along the Columbia River in the southwest portion of this county near the towns of Hunters and Cedonia indicate that sharp-tailed grouse may still occur in this area in limited numbers.

Lincoln County.—Since much of this county still remains in range land due to the channeled scabland areas which are in most cases too rocky to plow, sharp-tailed grouse occur in scattered populations throughout the county. Sage hens (*Centrocercus urophasianus*) are also present in limited numbers. Sharptails can be found in the following localities: Hawk Creek and breaks near Bachelor Prairie; North Telford Area (a level sage-brush country interspersed with Ponderosa pine (*Pinus ponderosa*), potholes and a few deep draws); Lake Creek Area (from Creston southwest to Irby); Connawa Area; and other breaks along the south side of the Columbia and Spokane rivers.

Recent records of grouse are as follows: Roosting sites seen near Wall Lake, March 17, 1949; twelve seen 5 miles south of Creston Butte on Sinking Creek, July 15, 1949 (H. A. Hansen). Two hundred or more birds wintered on the Jos. Long Ranch on Lake Creek at south end of Little Twin Lake, 1949-50. (Jos. Long). The extremely cold weather and deep snow concentrated the grouse into this stream valley where alders, willows and shrubs are abundant.

Grant County.—A few sharp-tailed grouse are reported to occur in the scabland along the east side of the Grand Coulee south of Electric City (Ralph Schwindel). Larrison (1942) states that a small group of sharp-tailed grouse have resided for the past several years in the barren sagebrush region immediately southeast of the southern end of Moses Lake. Three were seen by him in late March, 1940, and he had additional records from that area at the time of his writing.

Douglas County.—A brood of 4 young about 6 weeks old were observed one mile northwest of Delrio, July 21, 1949 (Yocom and Hansen). A few birds are reported to be found near Jamison Lake at the upper end of Moses Coulee and along the breaks of the Columbia River as far south as Waterville (Schwindel). The largest concentrations appear to occur, however, along the north boundary of the county in Straw Canyon and China Creek. A small flock was observed in 1949 on the Steveson Ranch, about 10 miles northeast of Delrio (W. W. Steveson). Five sharp-tailed grouse were seen on the Starkel Ranch, 2 miles west and 2½ miles south of Delrio, 1949 (Ben Starkel).

Okanogan County.—Sharp-tailed grouse were formerly common in the Similkameen River Valley along the International boundary; a few may still persist in that area (Steve Krusouff). Two pairs were seen at the base of Cayuse Mountain about June 1, 1950. There are a few grouse in this area; formerly this country was more thickly populated with homesteaders hence

there were more grainfields interspersed throughout the rangeland. This undoubtedly accounted in part for the reported abundance of these birds about 20 years ago (D. D. Catlin). A flock of 40 or 50 sharp-tailed grouse were seen on the west side of the Okanogan River along a small stream just south of Tonasket, December 20, 1949 (Roy Toole). A road-killed juvenile bird was found 5½ miles east of Tonasket on the Tonasket-Republic Road, July 21, 1949 (Yocom and Hansen).

Probably the best sharp-tailed grouse range still remaining in the State is the triangular shaped plateau located south of Omak, west of Goose and Omak lakes, north of the Columbia River and east of the Okanogan River. Approximately seventy-five birds were seen on the bench land north of the Columbia River about 1½ miles northwest of Bridgeport. The grouse were flushed from an oats field and were in flocks of 20 or more individuals each, latter part of July, 1949 (Eric Frangen). A road-killed juvenile bird was found 2 miles north of Duley Lake, and a female and four young (about 10 weeks old) were seen approximately one mile south of the Moose-Duley Road and the Goose Lake-Duley Road junction, July 27, 1949 (Donald S. Galbraeth and Yocom). A female and 3 young (about 2 weeks old) were seen near Karter on the breaks of the Columbia River, southeast of Goose Lake, June 14, 1950 (Yocom and Hansen). Seven were seen near Buffalo Lake, in August, 1949, and a flock of approximately 125 birds was seen along the Columbia River near Belvedere during the winter, 1949-50 (Schwindel).

Suitable habitat for sharp-tailed Grouse exists in the Methow Valley at the present time. John H. Mandery, Gamekeeper for the State of Washington Department of Game Methow Game Range, and Protector George McDaniels have observed grouse for several years in the Pearrygin Lake Country. Flocks of 12 to 30 were seen throughout the winter of 1949-50 on open hillsides northeast of Pearrygin Lake; nine were flushed from under an Amelanchier bush on Section 32, T35N, R22EWM, September 27, 1950 (Mandery). Twenty-five were seen on Section 30, T35N, R22EWM, December 29, 1950 (George McDaniels). A flock of 31 was seen in Section 7, T33N, R23EWM, first week in January, 1951 by John Galbraeth; flocks of 5 to 25 have been seen throughout January and February 1951, in Section 25, T35N, R21EWM (Mandery). Twelve were observed on 2, 3 and 4, April, 1951, southfacing slope north of Pearrygin Lake, NE ¼, Section 36, T35N, R 21EWM. Both Blue Grouse and Sharp-tailed Grouse were seen in the same general area (Byron and Dorothy Schottelius). There were estimated to be about 50 birds that wintered in the Pearrygin Lake Area during 1950-51.

Klickitat County.—Five or six were seen in the breaks 20 miles northwest of Roosevelt on the White Creek Ranch, 1949 (J. B. Gage).

Ray Meyer, Soil Conservation Service, Goldendale, Washington, furnished the following information on grouse in Klickitat County. None of the residents of Goldendale whom he questioned have seen this species in that vicinity for the last ten years. Harry Bryant of Goodnoe Hills near the

Columbia River observed a flock of 10 to 15 birds about 1940. The reports for Bickleton and the area south of there were similar: A flock was seen near Wood Gulch about 12 years ago; a few known to be in the area north of Sundale and a flock of about six seen above the Gorge between Roosevelt and Sundale about 1940. A small flock was seen on Alder Creek about 7 miles southeast of Bickelton, 1945, by N. B. Mattsen. The eastern portion of Klickitat County is sparsely populated. Even here sharp-tailed grouse had not been seen for four or five years by people reporting. An Indian told Meyers that he may have seen a small flock of five birds in the summer of 1949. They were off some distance but he knew that they were not Hungarian Partridge which are common in this area.

REFERENCES

BENT, ARTHUR CLEVELAND 1932—Life histories of North American Gallinaceous birds. Smithsonian Institution United States National Museum Bulletin 162: 490 pp.

BERNARD, ROBERT J. 1947—A history of Turnbull National Wildlife Refuge near Cheney, Washington. Unpublished thesis in History, University of California, Berkeley. 144 pp.

BRETZ, J. HARLAN 1928—The Channeled scablands of eastern Washington. Geographical Review 18: 446-477.

LARRISON, EARL J. 1942—Strange behavior of a sharp-tailed Grouse. The Murrelet 23(3): 79.

YOCOM, CHARLES F. 1943—The Hungarian partridge *Perdix perdix* Linn. in the Palouse Region, Washington. Ecological Monographs 13: 167-202.

The Foods of Fur Animals of the Patuxent Research Refuge, Maryland[1]

Leonard M. Llewellyn and Francis M. Uhler
Patuxent Research Refuge, Laurel, Maryland

The food-habits materials that form the basis of this report were collected incidentally in connection with two fur animal investigations at the Patuxent Research Refuge. One of these was a three-year (1943-1946) study to determine the fur productivity of a 1000-acre tract of submarginal land on the Refuge (Uhler and Llewellyn, 1952), and the other, a project on the biology of fur-animal populations, was begun by Llewellyn in 1947 and is still in progress.

The Area

The Patuxent Research Refuge of the U. S. Fish and Wildlife Service is a 2650-acre area devoted to wildlife research. It is located in the Patuxent River Watershed in Prince Georges and Anne Arundel counties, Maryland, midway between Baltimore and Washington. The section of the Refuge used for these investigations consists mostly of wooded bottomland of the Patuxent River. This flood plain is separated by low bluffs from irregular areas of nearly level terrace. Back of the terrace is upland consisting mostly of broad, flat hilltops reaching an elevation of 200 feet.

Most of the Refuge is forested, with many of the previously cultivated areas now covered by pine or sweet-gum stands. The floodplain forest is composed entirely of hardwoods. The terrace and upland forest consists either of mixed pine and hardwoods, hardwoods, or pure stands of pine. The latter are usually even-aged and are found in previously cultivated fields. A description of all habitat types on the Refuge is given by Hotchkiss and Stewart (1947).

Capture sites of the eight species of fur animals under discussion, plotted on a vegetational map of the Refuge, showed that four habitats were outstanding. A brief description of these follows:

Hedgerows, wood margins and roads.—This is the most productive habitat type. It includes considerable edge consisting of hedgerows, woods margins and roadsides. Many fields are bordered or cut up by hedgerows dominated by a variety of trees having a dense understory of shubs and woody plants. Similar vegetation is found along woods margins, woods roads and other openings in the forest. In these places, trees such as sassafras, persimmon,

[1] The writers wish to acknowledge the help of Lucille F. Stickel for analyzing part of the stomach material, Robert E. Stewart for identifying bird remains, William H. Stickel for help in determining certain mammalian and reptilian remains, and Robert T. Mitchell for help on invertebrates.

wild black cherry and sweet gum are common. The understory is composed mainly of smilax, blackberries, wild grapes, sumac and Japanese honeysuckle

Bottomland forests.—The bottomland forests include small tracts of nearly virgin timber as well as areas that have been cut over at some time. In the mature stands, beech is the dominant species. Tulip tree and sweet gum also occur in small, nearly pure stands. Other common trees are hornbeam, river birch, oaks, red maple and ash. A variety of shrubs, vines, and herbs occupy the understory.

Marshy lake-border—This habitat occurs around several artificial impoundments. These shallow-water areas have become vegetated with rice cutgrass, cattails, bullrushes, and burreed. Wildrice and a considerable number of other marsh and aquatic plants have also been planted. The habitat is important for muskrat and also makes good feeding areas for raccoon and mink.

Cultivated fields.—The fourth major kind of habitat consists of cultivated fields. Corn proved especially attractive to several species of fur animals. Corn fields were prominent on a study-area map upon which raccoon captures were plotted. Areas containing crops attractive to mice were frequented by predatory species.

MATERIALS AND METHODS

During three seasons of kill-trapping, all stomachs and intestinal tracts of fur animals were preserved and later analyzed. There were 279 usable units. In the subsequent project, which dealt mainly with raccoon populations on the Refuge, many scats were collected from live-traps. This method of securing food-habits material had advantages over both kill-trapping and promiscuous collecting of scats since, without having to sacrifice animals, there was no doubt about the source or date of the study material. Kill-trapping resulted in only one sample collected from an individual, but live-trapping, sometimes of animals re-trapped many times, made possible numerous scats from an individual. A total of 560 scat samples was collected in this manner. Fall, winter ,and spring seasons were generally well represented in samplings for the different species. but summer months have scant representation except for the raccoon. Seasons denoted in the graphs for the various animals studied are not uniform as to months included because distinct changes in diet occurred during different months in different fur bearers.

Data on foods are expressed in percent by volume and frequency of occurrence. Scat remains were estimated in volumetric percentages to make the data comparable to those obtained from stomach analyses

RACCOON—Procyon lotor lotor

The raccoon was captured on the study area in all of the habitat types represented. It is most abundant in forested bottomland where it is never far from water. It frequents farm lands and though it is occasionally taken in pure pine stands, this habitat is probably used only for travel. As would be

expected, much of the animal's food is associated with the forested bottomland or edges such as fences and hedgerows.

A total of 520 usable samples of raccoon stomachs and scats was analyzed. They were reasonably well-distributed over the year, although most of the stomachs were taken in the winter season. Scats were collected in every month.

Food of the raccoon is varied and the kind used is determined largely by availability. When preferred foods are scarce or absent, this animal is particularly adept at subsisting on items that ordinarily would be insignificant in its diet.

Plant material (48%).—In summer, fall, and early winter, plants provided the bulk of the raccoon's diet (Fig. 1). The use of plant items became considerable in June and July, reached a high in November, and then tapered off through March. An all-year summary of volumetric percentages showed seven principal items of plant food. These were corn (8%), wild grapes (8%), wild black cherry (7%), acorns (8%), persimmon (4%), pokeberries (4%), and blackberries (3%). These seven made up almost all the plant material, 42 percent out of a total of 48 percent. Most other items showed up sporadically or were prominent only for short seasons.

Serviceberry (*Amelanchier* spp.), ripening in June, usually was the first fruit of the year obtained. Though not a major item, it was used every year. This was true also of the sweet cherry (*Prunus avium*) which ripens a little later and of which there are a few trees locally. A few unripe wild black cherries (*Prunus serotina*) were eaten in June. In July species of *Rubus* ripened, first the dewberries and later the blackberries. They constituted a major part of the raccoon's bill-of-fare and were eaten as long as the supply lasted. As long as blackberries were plentiful, their seeds were common in scats. Blueberries (*Vaccinium* spp.) and huckleberries (*Gaylussacia* spp.) were eaten in years when good crops of them were available. About the middle of August, wild black cherries were fully ripe and were eaten extensively until the supply was depleted early in the fall. Almost two thirds of the August diet consisted of this item. During this month raccoons started visiting corn fields. Both the sweet and field type of corn were used from the time they reached the milk stage until the supply was gone.

September, the month when fall foods begin to ripen, brought a greater variety of plant products, but the total of about 80 percent was nearly the same as for the preceding month. Wild grapes (*Vitis* spp.) and pokeberry (*Phytolacca americana*) comprised almost half of the food during this period. Grapes were taken from the time they started to ripen until the supply was exhausted late in December or early January.

Though a good crop of beechnuts (*Fagus grandifolia*) occurs only about once in five years in this region, usually a few trees bear some fruit each year, and this item is represented in raccoon food nearly every fall. In years of good crops, extensive feeding was noticed. The pawpaw (*Asimina triloba*) also is intermittent in productivity, but its quantity on the study area was too limited to be of importance.

One of the most important fall foods in this region is the persimmon (*Diospyros virginiana*). Raccoons started eating these fruits in September while they were quite unripe and astringent, and fed heavily on them in October and November. The high sugar content of this fruit appears to be a valuable winter conditioner for the raccoon. The persimmon, along with grapes and pokeberry, formed over half of the October diet. There is no doubt that corn was also used at this time, but since it was used regularly for bait in live-trapping, its occurrence had to be excluded in records of scat analyses.

Foods taken in November and December were largely the same as in October, with some items becoming less well represented as their supply dwindled. Acorns (*Quercus* spp.) were eaten in late fall and winter, and, when the crop was sufficient, were an important food. They appear to be valuable in helping young animals to mature and in putting both young and old in condition to withstand the critical months to follow.

In January, February, and March, the three main items were corn, acorns, and greenbrier berries (*Smilax* spp.). Smilax berries always appeared as a winter or early spring food when other items became scarce, or when the ground was snow covered. They apparently were a "last resort" in the diet and the extent of their use was in inverse proportion to the availability of other foods. During the months of April and May, the diet is practically devoid of plant materials.

Animal material (52%).—A much larger list of animal items—well over 100—was involved is the raccoon's diet. For this reason only the major items are shown in Fig. 1. The greatest volume of animal foods was taken in late winter and spring. In late winter, after most plant foods were depleted, many animals depended largely on insects. They turned over the duff and debris around the margins of woodland swamps, ponds, and streams picking up insects and other bits of food.

Among the lower invertebrates, crayfish (*Cambarus diogenes*) were the most important, and like snails, were eaten throughout the year. Spiders, though frequent, were low in volumetric measurements, partly because leg fragments were usually the only remains that persisted. Millipedes and bivalve molluscs were less frequently eaten.

During most of the year, insects were important as food. Of these, beetles (Coleoptera) made the largest contribution and at times composed almost a third of the diet. Ground beetles (Carabidae) and scarabs (Scarabaeidae) were taken most frequently. During the height of the Japanese beetle (*Popillia japonica*) period, these insects were eaten freely and some raccoons fed almost exclusively on them. For example, one scat contained parts of over 120 Japanese beetles—probably only a small part of the total eaten by the animal in a single night. The orders Hemiptera, Hymenoptera and Odonata were also well represented in the raccoon diet. Of the former, the various species of stink bugs (*Pentatomidae*) appeared most often. In the Hymenoptera, ants were found frequently but never made up much of the volume. Raccoons apparently dug up and destroyed yellow

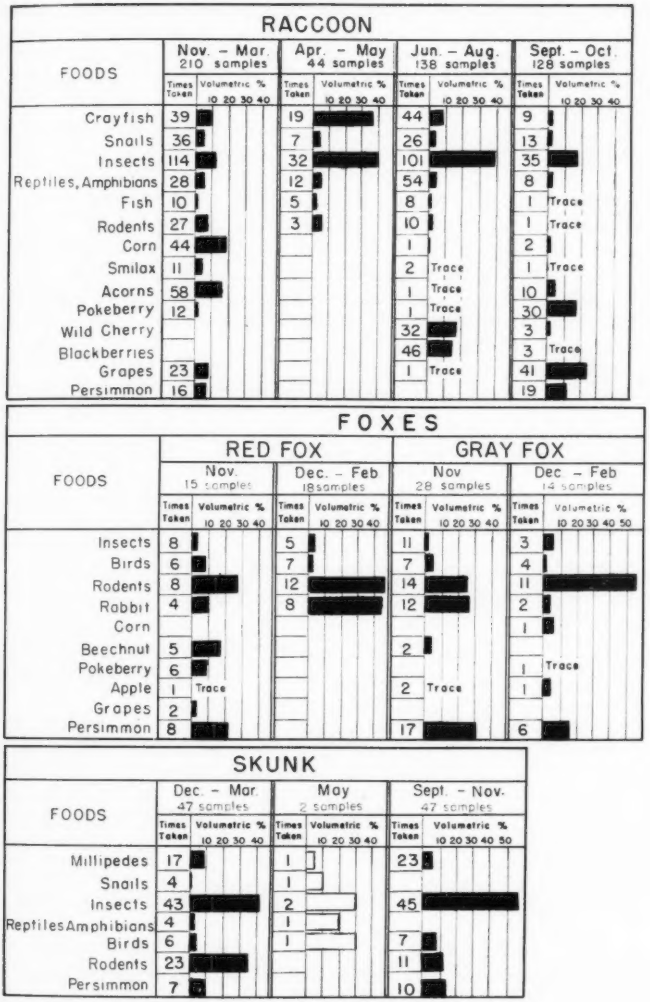


Fig. 1.—Seasonal foods of the Raccoon, Fox, and Skunk. (In instances wherein samples analyzed total less than ten, graphs are denoted in outline only, not by black bars.)

jacket (*Vespula* spp.) nests wherever encountered. Judging by the quantities of these insects found in many scats, most of the inhabitants of the excavated nests must have been consumed. The order Odonata was represented by several species of dragonfly naiads, often in considerable numbers. Grasshoppers (conspicuous in the diet during October), camel crickets, hellgrammite larvae, and fly pupae and larvae made up most of the representatives of other orders listed.

Cold-blooded vertebrates eaten consisted mainly of a few species of fish, salamanders, frogs and snakes. The remains of turtles themselves were not often found but their clutches of eggs apparently provided substantial meals, as many turtle nests were found destroyed and fragments of shells were found several times in scats. Birds constituted only a small portion both in volume and occurrence. Some of the few traces of bird may have been carrion or stray feathers that the raccoon picked up. Rodents found most frequently were wood mice (*Peromyscus leucopus*), pine mice (*Pitymys pinetorum*), and meadow mice (*Microtus pennsylvanicus*). Rabbit remains (*Sylvilagus floridanus*) were found in few stomachs and in one scat. Some of the rabbit material in the stomachs might have been bait, although this was generally eliminated.

RED FOX—Vulpes fulva

Only a comparatively small sampling of food-habits material was secured for the red fox (Fig. 1). A total of 26 stomachs and 7 scats were examined, practically all being taken in the months of November, December, and January. Foxes were rarely taken in live-traps and scats collected at random are usually hard to identify accurately.

Plant material (17%).—In the fall, the red fox made considerable use of fruits, berries, and other plant items (Fig. 1). Field examination of fox scats during this season showed that many of them contained 100 percent of either persimmon, pokeberry, or grape. Apparently persimmon was a favorite food of foxes as well as raccoons and other mammals; November analyses showed 23 percent of this fruit. In the fall of years when beeches bore heavily, stomachs were gorged with their nuts. The November average of 18 percent indicated in the diagram is exceeded in good years. The only other plant product eaten to any extent was pokeberry which totalled 9 percent. Wild grapes, apple, pear and corn were used to a varying, but generally minor, extent.

Animal material (83%).—Most of the red fox's food for the entire year is of animal origin. The most important item, according to volume, appeared to be rabbits, with an average of almost 50 percent. Rodents occurred more frequently, but made up little more than 25 percent of the volume. The rodents consisted mainly of meadow mice, pine mice and wood mice. Gray and flying squirrels, house mice, and a shrew were also eaten. Birds, including mourning dove, junco, fox sparrow and domestic chicken, were found 13 times for a volume of 6 percent. In two instances the domestic chicken consisted of parts of feet or head feathers and was probably offal. Insects

did not rank high in percentage (1%), but in November, crickets and grasshoppers were found in about half of the stomachs.

GRAY FOX —Urocyon cinereoargenteus cinereoargenteus

Foods of the gray fox are well-represented only by the single month of November in the present study. Twenty-nine November stomachs and one scat were suitable for tabulation. December was represented by eight stomachs and January and February together by seven, making 44 in all.

Plant material (30%).—The kinds of foods eaten by the gray fox during this study do not differ materially from those of the red fox but their frequencies and volumes diverge, probably because of distinctive habitat preferences (Fig. 1). Persimmon was the most important plant item with a 21 percent total. It made up a fourth of the November diet and a third in December but the supply was just about exhausted in January (2%). Corn, pear, apple and beechnut were the only other foods of plant origin.

Animal material (70%).—Rodents made up about half of the volume of the year-round food. In the seven January and February stomachs, mice constituted 83 percent of the entire food. In contrast to this, rodents constituted about a fourth of the November and December total. Though no rabbits were found in gray-fox stomachs during the January-February period, this was probably because sampling was limited. Rabbits made up only 5 percent of the volume for December, but were well-represented in November (27%). Birds and insects constituted most of the remainder of animal food. Birds composed 7 percent of the diet in November but were negligible in the other two periods. Insects were best represented in December (13%), were fewer in November (3%), and were down to 2 percent in January-February. One November stomach contained part of the remains of a raccoon, presumably carrion.

UNDETERMINED FOXES

A number of fox scats were collected at times when there were no tracks or other means of determining whether they were from the red or gray species. About half of those collected in winter showed rabbit. Rodents were found in practically all scats for winter, spring and early summer. Meadow mice were taken most commonly but wood mice, pine mice and house mice were also eaten. In late summer and fall, persimmons and grapes were present in quantities. Corn, pokeberry, pear, apple, and beechnut were also noted in lesser amounts.

MINK—Mustela vison mink

It is usually difficult to get food-habits material from trapped mink because digestion is rapid. Frequently the stomach was empty and only digested blood was found in the intestines. Only six stomachs and four scats were suitable for tabulation. Since so little material was available, no graph has been prepared for this species.

Plant material.—No material of plant origin was found except a few

poison-ivy seeds (*Toxicodendron radicans*). These were found in a stomach that included remains of a flicker (*Colaptes auratus*) and were assumed to have been eaten by the bird.

Animal material.—One mink sample in March and another in December contained rabbit hair only. Five other winter samples had 100 percent rodent remains consisting of one meadow mouse, three pine mice, and one wood mouse. In the two additional stomachs examined, one contained flicker remains and the other had a beetle fragment.

NEW YORK WEASEL—Mustela frenata novaboracensis

Only one weasel stomach examined had food in it. It was obtained in December and contained the remains of a wood mouse and one bird feather. Of several scats that were examined, most of them contained fur of various small rodents such as wood mice, pine mice and jumping mice. The majority of scats collected from live-trapped animals contained what appeared to be blood, the origin of which could not be determined.

SKUNK—Mephitis mephitis nigra

Most of the food-habits material obtained for this species consisted of stomachs taken by fall and winter kill-trappings. Consequently, spring and summer months are poorly represented. A total of 63 digestive tracts and 33 scats were analyzed (Fig. 1).

Plant material (10%).—Only one plant item, persimmon, was found regularly and it averaged but 7 percent. Beechnut, acorns, corn, wheat, pokeberry, blackgum (*Nyssa sylvatica*), smilax and a few other fruits and berries were eaten much less frequently. Some plant matter eaten was apparently garbage.

Animal material (90%).—Apparently at least 80 to 90 percent of the skunk's diet was of animal origin. Insects formed almost half of the total and were most prominent in the fall. Though several kinds of insects were eaten, most of the material was from a few groups. About 20 percent consisted of beetles, with scarabs such as June beetles (mostly larvae) and Japanese beetles (mostly adults) leading the list. Ground beetles were also found frequently. The next highest group (11%) was made up of grasshoppers and crickets. A large number (5%) of true bugs (Hemiptera), chiefly stink bugs, was eaten. In late summer and fall, it was evident that in several instances the skunk had dug out yellow-jacket nests and eaten the occupants. Rodents, mainly wood mice, meadow mice, and squirrels comprised 15 percent of the diet and eight occurrences of rabbit totalled 5 percent. It is thought that most of the rabbits and squirrels eaten were picked up as carrion, road kills, or hunting cripples, but remains of small rabbits that could have been nestlings were found in two scats. Birds were found in fourteen stomachs or scats and made up 7 percent of the volume. None of these were nestlings and no eggs were found. It would be difficult to say

how many of the bird records represented carrion—or even stray feathers that the animals may have picked up. One box turtle, one king snake, and several undetermined snakes and salamanders were eaten. Millipedes were found frequently in fall and winter and often made entire meals. Spiders appeared frequently, and centipedes occasionally, but their remains consisted mostly of leg fragments so their volume was low.

OPOSSUM—Didelphis virginiana virginiana

Several interesting trends were observed in examination of the 37 stomachs and 66 scats of opossum collected during this study (Fig. 2).

Plant material (14%).—The use of food of plant origin started in June and July, when dewberries and blackberries made up almost a fifth of the food. In September and October, persimmon, wild grapes, and apple raised the percentage to almost a fourth of the total. November showed the highest (32%) consumption of vegetable food when grapes comprised 15 percent and pokeberry and persimmon each 6 percent. Smilax, corn, and apple appeared in small amounts. In December the total dropped off (16%) with the only major item being grapes (14%). From January to April only minor occurrences of smilax, corn, and blackgum appeared. Other plant products encountered in lesser amounts at various times included beechnut, nightshade (*Solanum nigrum*) and ground-cherry (*Physalis* sp.).

Animal material (86%).—A third of the yearly animal dietary was made up of insects, with beetles (17%) being eaten most. Scarab and carabid beetles showed the greatest frequency of occurrence. Orthoptera, mainly crickets and grasshoppers, made up 7 percent followed closely by Hemiptera (6%)—mostly pentatomids. Snails of at least six species were well-represented with 10 percent volumetrically and 47 occurrences. The opossum was found to have eaten more millipedes than any other fur animal studied. They totalled 9 percent of the volume and 27 occurrences. Crayfish amounted to 6 percent, spiders one percent and centipedes one percent.

Among the vertebrates eaten, rodents led with a yearly proportion of 10 percent. The 25 occurrences of rodents were mostly of wood, meadow and pine mice, and two squirrels. Several shrews were also taken. There were 25 occurrences of birds for a volumetric percentage of seven. These included a variety of species, but usually only a few feathers remained as clues. It is difficult to see how opossums could have taken many of these birds alive, since in most instances they were neither ground-roosting nor ground-nesting species, so it must be assumed that the birds were either sick, injured, or carrion. No bird eggs were noted and only one bobwhite quail was found. A few frogs, seven snakes, and a few salamanders and fish were recorded.

HOUSE CAT—Felis domestica

The house cat, though not ordinarily classed as a fur animal, is often a predatory species. Predation by both feral and domestic cats is often claimed

to be significant to wildlife management. During this study 15 digestive tracts and 25 scats were collected, mainly during the fall and winter period (Fig. 2). Only slightly more than 2 percent of food of vegetable origin was found and this was believed to be garbage.

Animal material (98%).—During the year as a whole, rodents were by far the most important food, comprising over three-fourths of the diet by volume and almost half of the occurrences. They were mostly meadow, pine and wood mice. One stomach contained at least eight meadow mice. The remains of several squirrels were found. One of the latter contained lead shot and was probably a hunting casualty. The other major food item was rabbits, six of which were eaten. At least one of these was a young rabbit. More shrews were eaten by the house cat than by any other animal studied, and seven birds were noted. Insects, mostly grasshoppers and crickets, eaten in the fall amounted to 2 percent.

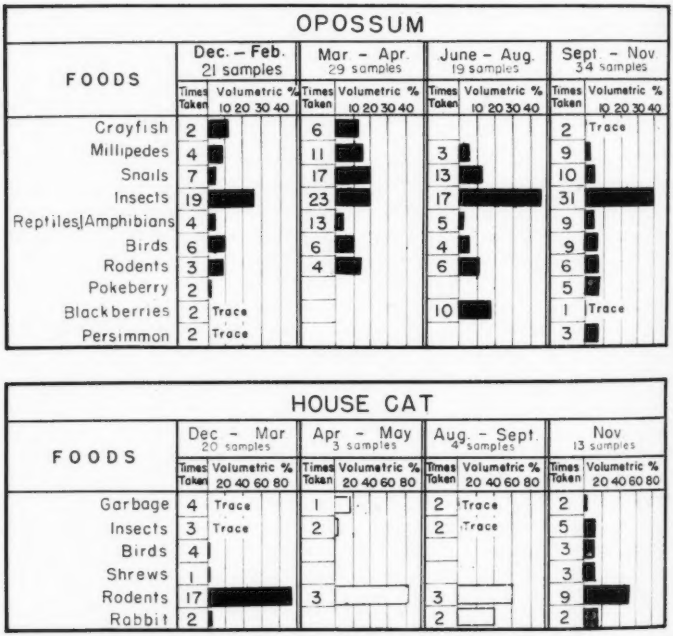

OPOSSUM
FOODS
Dec. – Feb. 21 samples
Mar – Apr. 29 samples
June – Aug. 19 samples
Sept – Nov 34 samples
Times Taken
Volumetric % 10 20 30 40
Crayfish 2 6 2 Trace
Millipedes 4 11 3 9
Snails 7 17 13 10
Insects 19 23 17 31
Reptiles Amphibians 4 13 5 9
Birds 6 6 4 9
Rodents 3 4 6 6
Pokeberry 2 5
Blackberries 2 Trace 10 1 Trace
Persimmon 2 Trace 3
HOUSE CAT
FOODS
Dec – Mar 20 samples
Apr – May 3 samples
Aug. – Sept. 4 samples
Nov 13 samples
Times Taken
Volumetric % 20 40 60 80
Garbage 4 Trace 1 2 Trace 2
Insects 3 Trace 2 2 Trace 5
Birds 4 3
Shrews 1 3
Rodents 17 3 3 9
Rabbit 2 2 2

Fig. 2.—Seasonal foods of the Opossum and House Cat. (In instances wherein samples analyzed total less than ten, graphs are denoted in outline only, not by black bars.)

MUSKRAT—Ondatra zibethica macrodon

Information on muskrat foods is confined wholly to field observations. No stomachs or scats were analyzed.

Plant material.—Native and introduced aquatics that were planted in the artificial impoundments for the benefit mainly of waterfowl were also used by muskrats. In some instances it was necessary to protect new plantings with wire until the vegetation had established itself. Some of the more important native foods used at the Patuxent Refuge by muskrats are bur-reed (*Sparganium americanum*), hairy arrowhead (*Sagittaria pubescens*), broadleaf arrowhead (*S. latifolia*), white waterlily (*Nymphaea odorata*), common cattail (*Typha latifolia*), and water-starwort (*Callitriche heterophylla*). Three-square (*Scirpus americanus*) and wildrice (*Zizania aquatica*), introduced from Southern Maryland, are used extensively. Introductions of both common and Asiatic wildrice (*Zizania latifolia*) had to be protected by wire enclosures to prevent complete eatouts. Hardstem bulrush (*Scirpus acutus*) introduced from Minnesota and native woolgrass (*S. cyperinus*) are also favorites. Rootstocks of another recent introduction, floating-leaf pondweed (*Potamogeton natans*), seems to be well-liked by muskrats. Muskrats living along the river utilize a variety of succulent plants with availability the apparent determining factor in kinds taken.

Animal material.—Although this species is primarily herbivorous there is evidence that animal material may be eaten frequently and at times in considerable quantity. Shell middens were found along the Patuxent River where muskrats had eaten a freshwater clam (*Unio complanata*).

SUMMARY

Approximately 300 digestive tracts of fur animals obtained mostly during the winter trapping season and 560 scats from animals live-trapped on the Patuxent Research Refuge near Laurel, Maryland, were analyzed. The resulting data are summarized and a brief description of the area and important habitat types is given. The animals studied include the raccoon, red fox, gray fox, mink, New York weasel, skunk, opossum, and house cat.

REFERENCES

HOTCHKISS, NEIL AND ROBERT E. STEWART 1947—Vegetation of the Patuxent Research Refuge. Amer. Midl. Nat. 38(1): 1-75.

UHLER, FRANCIS M. AND LEONARD M. LLEWELLYN 1952—Fur Productivity of Submarginal Farmland. Jour. Wildlife Management 16(1) Jan. 1952: 79-86.

Ecology and Helminths of the Osage Wood Rat, Neotoma floridana osagensis, Including the Description of Longistriata neotoma n. sp. (Trichostrongylidae)*

Melvin F. Murphy

Department of Zoology, Oklahoma A. and M. College, Stillwater

The Osago wood rat, *Neotoma floridana osagensis*, was described as a subspecies by Blair in 1939, and since that time nothing has been published on either its ecology or parasites. Blair (1939a) used the common name Osage wood rat for the animal in his original description, but, in his later paper on the mammals of Oklahoma (1939b) he referred to it as the eastern wood rat. It is the opinion of the writer that the original common name should be used, not only for its priority, but also because of the quite desirable similarity of the common and subspecific names.

Up to this date the literature on the Osage wood rat consists merely of the original description and a few distributional records. Studies of the literature on closely related species afforded some understanding of the habits, activities and parasites of wood rats in general, which was used as a basis for comparison with the Osage wood rat.

Wood rats, commonly referred to as pack rats, trade rats, and occasionally as bush rats, are confined to the North American Continent and have been known for 200 years. They were first reported by Peter Kalm in 1749, who cited John Bartram of Philadelphia as authority for the statement that he saw a large number of rats living among the rocks and cliffs in the Blue Mountains of Pennsylvania. He further stated that these rats came out only at night and were extremely vociferous. Ord (1818) sent a short description and a figure of a wood rat taken from eastern Florida to the Philomatique Society of Paris. The description and figure were given under the scientific name of *Mus floridanus*. De Blainville, who prepared the account for publication, questioned the generic name *Mus*. Meanwhile, in 1825, Say and Ord had discovered the peculiar dental characteristics of the species and published a diagnosis of a new genus *Neotoma* with *Mus floridanus* as the type. Merriam published two papers, one (1894a) on the revision of the genus *Neotoma* and the other (1849b) on the diagnosis of the subfamily Neotominae with a synopsis of the known species in the genus *Neotoma*. Goldman (1910) did the last extensive work on this group. He revised the genus, gave its geographical distribution, prepared keys for determining species, and submitted photographs of skulls to illustrate structures useful in identification.

* Contribution No. 169 from the Department of Zoology, Oklahoma A. & M. College, Stillwater.

The literature on the various species within the genus *Neotoma* is quite extensive. It consists mainly of short articles on some phase of the ecology or life history of particular species, but these may be fitted together so that they reveal a fairly complete composite, generalized life history.

Besides these short articles, there are three excellent publications, each of which gives a detailed account of a separate species or subspecies. Vestal (1938) published his work on *Neotoma fuscipes annectens* in the Berkeley Hills, California, giving not only a fairly complete life history of this subspecies but also its biotic relations. He gives a detailed account of the activities of the wood rat throughout a period of one year. His study area was 24.8 acres in size and included a total of 572 dens of which 516 were inhabited. An extensive manuscript was published by Poole (1940) giving his findings on *Neotoma magister* in Pennsylvania. His work was concerned with the activities of this wood rat in the field as well as in the laboratory. A third publication by Vorhies and Taylor (1940) was on the subspecies *Neotoma albigula albigula* and is the most extensive and comprehensive of all. The complete life history and ecology of this subspecies were given, and also the relation of the wood rat to the grazing problems involving domestic animals in Arizona was determined.

A review of the literature on the internal parasites reported from the genus *Neotoma*, showed that little research had been done. Only seven different species of helminths have been reported for all the species and subspecies of wood rats. Only a single species of internal parasite has been reported from *Neotoma floridana*. Hall (1916) reported *Syphacia obvelata* (Rudolphi, 1802) Seurat, 1916, in *Neotoma mexicana fallax*, and named and described *Nematodirus neotoma* from *Neotoma mexicana fallax*, *N. desertorum*, *N. floridana baileyi*, and *N. cinera rupicola*. Stiles (1932) reported *Moniliformis* sp. from a wood rat in Florida the only acanthocephalan reported from the genus *Neotoma*. Tucker (1942) named and described *Nematodirus tortuosus* from *Neotoma lepida intermedia* and *N. fuscipes macrotis*. Chandler (1945) named and described *Trichurus neotomae* from *Neotoma fuscipes*. *Andrya neotomae* was named and described by Voge (1946); this is the only cestode reported for this genus. Tiner (1948) reported *Rictularia* sp. from the genus *Neotoma*.

Since Payne County, Oklahoma lies well within the known limits of distribution of the subspecies *N. f. osagensis*, it was decided to use this area as a unit within which to study its ecology and helminths. This investigation was begun in January 1949 and continued until May 1950.

ECOLOGY OF NEOTOMA FLORIDANA OSAGENSIS

Habitat.—The wood rats in the Stillwater area have a preference for two major type habitats—the post oak-black jack ravines and the fringed forest ravines. In addition to these, a few rats have been observed living in upland oak wood and in upland locust plantings, but, due to their insignificance in the ecology of the wood rat, these habitats will not be discussed.

Post oak (*Quercus stellata*)-black jack (*Q. marilandica*) ravines are prevalent in this region. They are dominated by these two species of trees and are characterized by having intermittent streams. On either side of such ravines there are usually projecting rocky ledges that afford ideal protection for wood rat dens. The intolerant plants in the oak ravine are yellow oak (*Q. Muhlenbergii*), bur oak (*Q. macrocarpa*) and native juniper (*Juniperus virginiana*). The tolerant species are smooth sumac (*Rhus glabra*), dwarf sumac (*R. copallina*), poison ivy (*R. toxicodendron*), wild grape (*Vitis cordifolia*), common green briers (*Smilax rotundifolia* and *S. pseudochina*) and buckbrush (*Symphoricarpos orbiculatus*).

The fringed forest ravines are quite different from the post oak-black jack ravines in a number of respects. They have constant or intermittent streams, depending upon the time of year and amount of rainfall. These ravines are at a lower level than those of the post oak-black jack type and the soil of these has a higher moisture content. There are very few rocks here, but, when they are present, they are well covered with soil, leaving no spaces for the wood rat to construct a den. The intolerant plants in the elm ravine are the Kentucky coffee tree (*Gymnocladus dioica*), cotton wood (*Populus deltoides*), native pecan (*Carya illinoensis*), and black walnut (*Juglans nigra*). The tolerant species are the smooth sumac, dwarf sumac, poison ivy, wild grape, common green brier, buckbrush, dogwood (*Cornus asperifolia*), redbud (*Cercis canadensis*), black willow (*Salix nigra*), and wild plum (*Prunus americana*).

These two types of habitat were surveyed equally well but there was a great difference in the number of wood rats collected from each. Each type habitat was visited alternately, and the same amount of ground was covered on each occasion. In the post oak-black jack association 39 wood rats were trapped, while only 13 were taken from the fringed forest habitat. The wood rat probably prefers the oak habitat to the fringed forest habitat for the following reasons: 1. The soil moisture content is lower. 2. There are more projecting rocky cliffs which the wood rat seems to favor for nesting sites. 3. There is a greater abundance of acorns.

The den.—The dens or houses of the wood rat vary widely in size and in the sites chosen for their construction. In the post oak-black jack ravines the dens are usually built under projecting cliff rocks and only the entrances into the houses can be seen. These entrances may be very elaborate, consisting of openings through extensive piles of materials such as twigs, leaves, bark, stones, bones, and dried droppings of cows, horses and other animals. On the other hand, in a similar situation, the entrances to the dens show only a few exposed sticks and leaves.

In some instances, even though projecting cliff rocks are available, the wood rat avoids the rocks and constructs its den in the open. This type of den is similar to the ones built in the fringed forest ravine habitat and will be described subsequently for that habitat.

The dens in the fringed forest ravine habitat, where rocks are few in number, are quite different from those in the post oak-black jack ravine habi-

tat. In this environment the wood rats build their dens either around fallen trees, in brush piles, at the base of large trees, or under thick tangles of wild grape and green brier. These houses are constructed from approximately the same kind of materials that were used in building the dens in the other type habitat, but are usually much larger in size. Some of these dens measure as much as twelve feet in length by six feet in width and may have a height of over three feet.

The third type house, of which only three found, is the aerial den, and may be found in either type habitat. The first den of this type was found three feet above ground in a juniper tree. It was constructed of juniper needles and oak leaves. This den was dissected and found uninhabited. The second one observed was constructed in a locust tree and the third in a tangle of *Vitis* and *Smilax*. These two dens consisted of leaves, sticks, and other trash and both were occupied.

The number of openings into a den is variable and it seems to be correlated to some degree with the surroundings in which the den is constructed. The dens associated with rock ledges usually have only one entrance, although several dens were observed that had an additional entrance. Whenever a den had more than one entrance, there was a larger space beneath the rock. This additional space apparently permitted the construction of another entrance. The dens having the greater number of entrances were those that were not associated with the rock ledges. In these there are usually four entrances on various sides of the den which enable the rat to enter or leave from almost any direction. These additional entrances are undoubtedly related to the protection of the wood rat from its enemies.

The dens that were studied in the Stillwater area were not always occupied by wood rats. Only three wood rats were trapped in one area where 16 dens were found. In another area of twelve nests, three rats were taken. Only 55 specimens were trapped from a total of 241 dens in all areas. On the basis of this data it is probable that only about 23 percent of the dens were occupied. This is an exceedingly low den-rat ratio as compared with the study made by Vestal (1938) for *Neotoma fuscipes*. His area included 572 dens of which 516 were occupied.

However, in the fall of 1949, it was noted that many of the uninhabited dens were being reoccupied, and field observations and trapping during the following spring verified the findings and indicated that the wood rat population was increasing.

The most plausible explanations for the low den-rat ratio for the year 1949 are: 1. Wood rats may be cyclic as to abundance and they were probably at a low ebb in their cycle. 2. The unusually hard winter that preceded this investigation may have killed off numerous wood rats. 3. Sufficient food may not have been stored to carry them through the unusually severe winter. 4. Some epizootic may have reduced their number. 5. It may be a normal condition, of which no accurate information has been obtained, due to predator pressure.

As a result of both the survey and dissection of the dens, it was found that many of the uninhabited dens were occupied by animals other than wood rats, and in many instances these animals lived in association with the wood rats. Table I lists the commensals or occupants other than rats found in each of 25 occupied and 25 unoccupied dens.

TABLE I.—Animal inhabitants of fifty *Neotoma* dens

Type of Animal	Frequency 25 Occupied Dens	Frequency 25 Unoccupied Dens	No. per Den
Invertebrate			
Ants	17	21	Numerous
Daddy longlegs	11	12	1 to 10
Spiders	9	13	1 to 10
Sow bugs	7	11	1 to 5
Millipedes	4	9	1 to 10
Ground beetles	2	7	few
Bumble bees		2	few
Vertebrates			
Deer mice	3	8	1 to 2
Lizards	2	5	1 to 3
Cotton rats		3	1
Cottontail rabbits	1	2	1
Water snakes	1		1
Spotted skunk	1		1
Opossum	1		1

From Table I, it is apparent that there is little correlation between the arthropods of the occupied and unoccupied dens. Statistically, it would be impracticable to make calculations on the basis of these data for either the vertebrates or invertebrates since only fifty nests are involved. Nevertheless, it is interesting to note the variety of both invertebrates and vertebrates that inhabit or frequent wood rat dens.

The nest.—The den consists of two major parts, an outer area composed of sticks and trash and an inner area where the wood rat lives and builds its nest. The nest is usually near the center of the den, more or less spherical and measures approximately eight inches in diameter. It is usually constructed of several materials but occasionally only one item is used. The substances most commonly chosen for nests are grasses, shredded bark, bits of paper, string, rags and occasionally feathers.

According to Vorhies and Taylor (1940), it is the habit of some wood rats of another species to build subterranean nests beneath the surface dens. However, all the dens found by the writer have been on the surface of the ground or in trees.

Even though the nests are on the surface of the ground, they are still well protected. After severe rainfalls the inner portions of the dens and the nests are still dry and warm. This is due to the fact that the den is always built

where there is good drainage and the projecting cliff rocks or the twigs, leaves, bark, and debris making up the den keep the water from penetrating the nest.

General habits, including captivity.—The wood rat is a solitary animal. It occupies the den which it builds and apparently lives there alone except during the breeding season and when rearing its young.

The wood rat is active throughout the year although it apparently stays within its shelter on wet or extremely cold nights.

Although the wood rat is primarily nocturnal in habit, several instances of daytime activity has been noted. They have been seen especially in the late afternoon when traps were being set. Several wood rats were trapped about sunset but none was taken by this method during earlier hours. Consequently, it appears that, although there is daytime activity, it immediatedly precedes the dusk.

Trapping experience indicates that the wood rat is active during the early hours of darkness but without more evidence it is impossible to tell whether they are equally active during all hours of the night.

The activities of the wood rat are not confined entirely to the ground. On one occasion a wood rat was chased from its den in mid-afternoon. It immediately climbed one tree and then jumped, with the agility of a squirrel, to an adjoining tree. The capture of the wood rat was accomplished by climbing the tree and with the aid of two sticks it was lifted from its hiding place. Another wood rat, after being chased from its nest, ascended a tree and hid between the bark and pulp in a hollow formed by decay. After considerable harassing, the wood rat jumped to the ground some 15 feet below and made its escape into the underbrush.

Wood rats have been kept successfully in the laboratory which made it possible to observe them in captivity. Three wood rats, two females and one male, were captured in August 1949. One female was destroyed, after giving birth to four young, because of poor physical condition. The remaining two are still alive aften ten months in captivity. Another male, taken in February 1950 is also living after three months.

In the laboratory the activities are in many respects similar to those in the field. The rats sleep most of the day unless disturbed and show greatest activity during the first few hours of darkness. Their activities between midnight and morning have not been observed.

The two females showed a tendency toward giving up some of their wildness in captivity. They would come to the door of the cage for their food but never acquiesced to the extent of taking food from the hand of the feeder. The male, on the other mand, was not as gentle as the females and would cower in the back of the cage when the door was opened.

The usual sites of food storage and defecation were at opposite corners, although the male insisted on storing his food in the center of the cage. The food pellets were always kept in a neat pile. Whenever the rats were fed they carried their food to the place chosen for storage and if their existing store was scattered about the cage, they immediately returned it to the storage area.

A few interesting observations were made concerning the tolerance of one wood rat for other members of the same species. On February 10, 1950, a male wood rat that had been kept in captivity for six months was placed with a female that had been in the laboratory an equal length of time. The female attacked at once. The male, sensing trouble, squealed, scrambled to the top of the cage and hung there, trembling. Each time he braved a descent, the female drove him back to his refuge but did not follow him there. After several hours had elapsed, the male was removed from the female's cage. His tail and ears were bleeding and he left many tufts of hair as symbols of the occupant's victories.

A similar experiment was repeated in March, but on this occasion a recently trapped male was placed with the same female. She attacked as before but this male cuffed her sharply on the head. She backed off a short distance and charged again. The male slapped her as before. With a sudden change in attitude and tactics, she retired to her corner, preened herself, and gently approached the male. No further antagonism followed and they lived peacefully together until they were separated a week later.

Food and food habits.—The methods used in determining the food and food habits of the wood rat in this region consisted of making observations of stored food and middens in the field, and making analyses of stomach content of trapped wood rats.

The food of the wood rat, based on the content of 55 stomachs, is almost entirely plant material. Only three stomachs contained any animal matter and then only in an exceedingly small amount. One of the three stomachs contained a scorpion tail, another a snail shell (*Succinea avara*) and the third had small pieces of partially digested grasshopper.

On the basis of stored food and middens, it was further determined that the early summer diet of the wood rat is mainly grasses. Later in the summer acorns, sumac bark, fruit of sumac, poison ivy and dogwood are apparently eaten.

The winter food seems to consist largely of acorns, sumac bark, and seeds of red bud, Kentucky coffee tree, and sumac. Acorns are eaten from the time they are available in the summer until the supply is exhausted in the early spring of the following year and they constitute one of the main winter foods.

The wood rat usually provides its habitation with some food storage but occasionally nests were dissected with no evidence of stored food. Consequently, it is assumed that food storage is a minor and, therefore, variable factor in the economy of the wood rat. The provisions hoarded are mostly acorns, Kentucky coffee tree pods, sumac seeds and short twigs of the sumac, approximately eight inches in length.

There is little indication that the regular food of the wood rat makes it an animal of direct economic importance, and only in a few instances did stored food give information to the contrary. In one instance, eight dens were dissected near a quail food patch in the Lake Carl Blackwell area near Stillwater. These dens contained a good supply of sorghum heads that had been looted

from the adjoining field. At another time a single den was located near a corn field. The nest did not contain corn but there were numerous cobs without kernels on the midden pile. It would be impossible to state with certainty whether the rat carried the cobs of corn to its den for food because the evidence is only circumstantial. It may have been attracted only to the cobs lying in the field which it carried to its den and later cast on the midden pile.

Midden piles are confined to the outside of the wood rat den and are quite common. They are composed largely of seed hulls, seed pods, barked twigs, and fecal pellets. Cahalane (1947) states that the size of the midden piles are indicative of the length of time that the wood rat nest has been occupied. Since some rats in this area store very little or no food, an old house may possibly have only a small midden pile; consequently, its value in this connection is questioned.

These wood rats apparently need no drinking water to survive, but they are not entirely refractory to it as shown by experiments. Many of the dens are situated so far from water that during periods of drought, the wood rat must either obtain water from succulent vegetation, dew, or as a by-product from the utilization of carbohydrates.

Several experiments were carried on in the laboratory to determine if water is necessary or essential to the wood rat. In August, one male and one female, immediately after capture, were placed on a diet consisting of full ration dog pellets and lettuce leaves. No water was offered these animals throughout the experiment and at the end of one month both rats appeared to be normal and healthy.

Subsequent to this test, the same two rats were used in another experiment. The lettuce leaves were discontinued in the diet and a bowl of water was placed in each cage. Several days, however, were allowed to elapse before the experiment was initiated in order to accustom the wood rats to the absence of vegetation and the presence of bowls of water. After this period the bowls were cleaned and 200 cc. of water were poured in each of them. A third bowl with the same amount of water was placed on top of one cage as a control. After 48 hours the amount of water remaining in each bowl was measured. The water outside of the cage was used to determine the loss from evaporation, and the amount used by the wood rats could be measured. This experiment was repeated three times. As a result of these, it was determined that the male used an average of 156 cc. of water in a 48 hour period and the female an average of 51 cc.

Throughout these experiments the wood rat had not been seen drinking water so that it was not known whether the water was consumed or used in other ways. The following procedure was tried in order to find out what use the wood rats were making of the water. The water was removed from the cage for two days and then the same containers with water in them were replaced. Both rats started to drink immediately, lapping the water in a catlike manner.

From these tests it is apparent that the wood rat will drink water if it is available, but it is not necessary for survival.

Reproduction.—Sexual activities and reproduction are important phases of study in the ecology of the wood rat, but because these animals are almost entirely nocturnal, there is little opportunity to observe them except with specialized techniques and equipment.

Some information concerning pregnancy and gestation was gained, however, by the dissection of trapped animals and by observations of pregnant females in the laboratory. Of eight females that were trapped between March 5 and April 15, 1949, four were pregnant. The uterus of each of the pregnant ones contained four embryos, although an embryo in one female appeared to be in the process of resorption. The embryos were divided equally in the paired horns of the uterus of each female, except where resorption seemed to be taking place. In this wood rat there were three embryos in the left horn and the one nearest the cervix was being resorbed.

On April 15, a female with a litter was collected and when chased from her nest, she had three young clinging to her teats. These young wood rats averaged 105 mm. in total length and 19.5 grams in weight. No attempt was made to rear the young to determine their growth rate.

A pregnant female also was collected in a live trap on August 6, 1949. It was retained in the laboratory and yielded further information on reproduction. The wood rat was placed on one side of a double cage. The adjoining half of the cage, separated by a solid partition, contained a non-pregnant female which had been trapped in a similar manner.

On entering the laboratory at 11:30 a.m. on August 15, 1949, it was noticed that the female wood rat had just given birth to a rat. The mother did not respond by running to the back of the cage as she sometimes did when she was approached, but continued licking and cleaning the young one without acknowledging the writer's presence. After cleaning the young rat thoroughly, the female walked to a back corner of the cage, leaving the first born near the front.

The first indication of a second parturition was muscular contractions of the abdominal region. At this time she was in a position in which her back was extremely arched and her hind feet extended well forward and parted slightly. Her tail and hind legs formed a triangle which supported her body. Her front feet and head were held off the floor. Her head was bent down and her eyes were closed. In this position the second young was born at 11:34 a.m. She cleaned it by licking, as the young rat searched for a teat. After finding a teat the young attached itself and remained so during the following two births.

The third young was born with the mother in a similar position except that her head was bent down until the crown rested on the floor. This presentation was at 11:36 a.m. just two minutes after the preceding birth. The mother immediately cleaned the third born which soon succeeded in attaching itself to a teat.

The female then moved, with her litter attached, to the other far corner of the cage. She appeared extremely exhausted and slept for a few minutes, in a standing position.

At 11:47 a.m. the fourth and final young was born with the mother in the same position. The afterbirth was eliminated following this birth which the mother ate as she cleaned the young. After clawing and crawling, this new born became attached to a teat.

The first born was still some ten inches from the mother and was crawling about in the excelsior. It seemed to have no set direction as it crawled but at 12:25 p.m. it found the mother and after some difficulty attached to the fourth and final teat.

During the rest of the afternoon the female rested either in a squatting position similar to the position during birth of the young or leaning to one side with her head resting on the floor.

Throughout the entire parturition the mother neither ate nor drank or gave any indication of the writer's presence. The female wood rat in the adjoining cage moved about nervously and made sharp thumping noises with her hind feet as if she were aware of something unusual happening in the adjoining cage.

The rats were not observed from 5:00 p.m. until the following morning. At this time two young were found in the finger bowl of water in which they apparently drowned. The remaining two seemed to be in good condition but the mother appeared tired and listless. She showed no desire for food or water but during the night she apparently visited the water dish and dropped the young into it either accidentally or intentionally.

On the second morning following the births no young rats could be found. A detailed search of the litter revealed a small piece of one head. The mother probably became frustrated during the night due to an uncontrollable disturbance in the laboratory and devoured the remaining two young.

The two drowned rats were measured for data on the size of *Neotoma* at birth, since no such information had been available. Measurements of one rat were as follows: total length, 94 mm.; tail length, 26 mm.; hindfoot, 12.5 mm.; weight, 12.3 grams, and those for the other rat were: total length, 93 mm.; tail length, 25 mm.; hindfoot, 12.5 mm.; weight, 12.2 grams.

Because of limited data on reproduction, no attempt is made to draw any conclusions on the number per litter, length of gestation or other sexual activities.

PARASITES OF NEOTOMA FLORIDANA OSAGENSIS

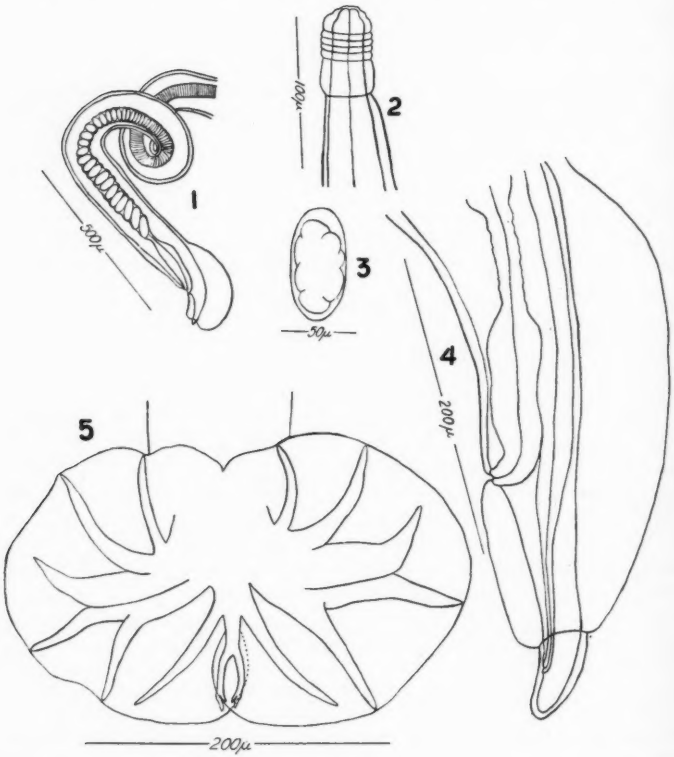
ENDOPARASITES

Longistriata neotoma n. sp. (Trichostrongylidae)

Description.—Worms small, delicate, spirally coiled, bright red in color and active when freshly collected; cervical inflation 0.055 to 0.065 mm. long by 0.035 to 0.041 mm. wide, marked usually with five annular striations; width of head, exclusive of inflation 0.015 mm.; cuticle of body inflated and marked with longitudinal striae, each showing cross striations; esophagus 0.285 to 0.345 mm. long by 0.038 to 0.045 mm. wide at its distal end; nerve ring

0.150 to 0.180 mm. from anterior end; excretory pore 0.210 to 0.255 mm. from anterior end.

Male: 3.0 to 3.8 mm. long by 0.086 to 0.120 mm. wide just anterior to bursa; bursa symmetrical, with two lateral lobes and one dorsal lobe; spicules similar, 0.395 to 0.410 mm. long, filiform, each ending in a single point; gubernaculum very rudimentary; ventro-ventral ray directed forward to margin of bursa and widely separated from latero-ventral ray; latero-ventral ray long and extending to margin of bursa; externo-lateral ray directed forward; externo-dorsal and externo-lateral only rays not reaching bursa margin; externo-dorsal



Figs. 1-5.—1. Posterior end of female showing typical coiling and eggs in uterus. 2. Anterior portion showing cuticular inflation with annular striations. 3. Egg at time of oviposition showing segmentation. 4. Posterior end of female showing ovejector, inflated cuticle and retractile tail. 5. Ventral view of bursa showing position and size of bursal rays.

ray long, originating from dorsal ray; dorsal ray divided for half its length, each branch bifurcating again at the tip, the outer member being slightly longer and thicker.

Female: 4.0 to 5.7 mm. long by 0.100 to 0.120 mm. wide at level of ovejector; ovejector well developed, single, 0.103 to 0.135 mm. long; distance from vulva to anus 0.110 to 0.131 mm.; anus to tip of tail 0.037 to 0.041 mm.; tail ends in a blunt point which may be retracted into a prepuce-like sheath; eggs very uniform in size, average 0.070 mm. long by 0.033 mm. wide.

Location: Small intestine.

Locality: Sec. 18-T19N-R1E Payne County, Oklahoma.

Type specimens: Holotype No. 37170, Smithsonian Institution; *Allotype* No. 37171, United States National Museum, Collection No. 37172 Washington 25, D. C.

The measurements were taken from ten live males and ten live females. The nerve ring was difficult to identify and was observed in only six of the twenty specimens. Twenty percent of the 50 wood rats collected were infected with this parasite.

It is extremely difficult to relax and uncoil these nematodes and as yet no good technique has been discovered. The best results were obtained by leaving the worms in a refrigerator in an isotonic solution at a temperature of 40° F. for several days. Thusly treated the males usually uncoiled fairly well but the females remained tightly coiled.

The specimens here described as *Longistriata neotoma* are, in many respects, similar to *L. dubia* (Travassos, 1921) but differ in having longer spicules, a shorter esophagus and no prebursal papillae.

Dikmans (1935) placed the genus *Longistriata* in the Heligmosomidae using Yorke and Maplestone (1926) as authority. Since no such family is given in Yorke and Maplestone, he apparently meant to place it in the subfamily Heligmosominae of the Trichostrongylidae as indicated in this reference. By using Dikman's key to the species in the genus *Longistriata*, this species keys to *L. beta*, but differs from it in consistently having a bilobed rather than a trilobed bursa.

Böhmiella wilsoni Lucker, 1943 (Trichostrongylidae).—These parasites infected 24 of the 50 wood rats and were the most common helminths of these animals. The only discrepancy encountered in comparing the worms from the wood rat with the original description of those from the squirrel was in the measurements of the females. It was found that the writer's specimens were from 11 to 14 mm. shorter, 0.10 mm. narrower and 0.14 to 0.22 mm. shorter in tail length. This constitutes a new host for the species.

Trichuris muris (Schrank, 1788) Hall, 1916 (Trichocephalidae).—These worms were found in 34 percent of the wood rats. These specimens differ from those described by Hall (1916) by being slightly larger, by having more cuticular vesicles and displaying a variable rather than a constant width between the transverse cuticular striations. Hall gives measurements for the spicular sheath, but in the writer's specimens the sheath was so variable as to size and shape that measurements were considered to be worthless. These dif-

ferences are not considered to be of sufficient magnitude to warrant a new species.

Andrya sp. (Anoplocephalidae).—Scolex diameter 0.900 to 0.975 mm.; sucker diameter 0.390 to 0.435 mm.; segments broader than long, progressively larger; genital pores irregularly alternating, situated in posterior third of lateral edge of proglottid; testes 0.042 to 0.050 mm. in diameter, numbering 50 to 70, and extending beyond aporal longitudinal excretory canal; cirrus pouch 0.180 to 0.225 mm. long by 0.085 to 0.093 mm. wide extending medially to inner wall of poral longitudinal excretory canal; seminal vesicle within cirrus sac; vagina dilated to form seminal receptacle measuring 0.270 to 0.300 mm. long by 0.120 to 0.150 mm. wide; lobed ovary situated slightly toward poral side of proglottid and just anterior to transverse commissure of excretory canal; vitelline gland posterior to ovary; eggs 0.032 to 0.042 mm. in diameter.

Location: Small intestine.

Two mature cestodes were collected on March 12, 1949, from the small intestine of a male wood rat. The condition of the worms prevented identification to species, but of the known species it most nearly fits the description of *Andrya macrocephala* Douthitt, 1915.

Taenia taeniaeformis (Batsch, 1786) Wolffhugel, 1911 Larva: (Taenidae).—This parasite was found in four wood rats. The specimens were confined to the hepatic tissue; three was the most found in any host. This constitutes a new host record.

ECTOPARASITES

The most conspicuous ectoparasites of this wood rat are bots or warble fly larvae of the genus *Cuterebra*. These are found beneath the skin of the throat and a fully developed larva may form a cyst the size of a marble. Only four of fifty wood rats were infested, but no rat harbored more than one specimen. The incidence of infestation by warble fly larvae in this study is identical to that found by Vorhies and Taylor (1940) in their survey of *Neotoma albigula*.

The fleas, ticks and mites are common parasites of the wood rat. The ticks and mites were determined to be species of *Ixodes* and *Eutrombicula* respectively. The fleas, in the family Dolichopsyllidae, presented a problem in identification and have been sent to the Rocky Mountain Laboratory at Hamilton, Montana.

SUMMARY

The Osage wood rat (*Neotoma floridana osagensis*) apparently prefers the post oak-black jack ravine to the fringed forest ravine because of lower moisture, better protective cover, and available food.

Only 23 percent of the 241 wood rat dens, either located in the open, under projecting rocky cliffs or in trees, were occupied.

The most common commensals and den associates of the wood rat are

ants, spiders, deer mice and lizards; other animals are found occasionally.

The nests of the wood rats, although not subterranean, are protected from adverse climatic conditions by rocky cliffs or den debris.

The wood rat is primarily nocturnal and is active throughout the year.

The wood rat is active in trees as well as on the ground.

Wood rats have been maintained successfully in the laboratory for a period of ten months and their activities were observed to be similar to those in the field.

The food of the wood rat as determined by storage, middens and stomach analyses is almost entirely vegetation.

The wood rat does not seem to compete directly with animals of economic importance in this region.

The wood rat will drink water if available but water is not necessary for its survival.

A female, that gave birth to four young in the laboratory, supplied considerable data on reproduction.

Longistriata neotoma infected 20 percent of the 50 wood rats collected and is described here as a new species.

The most common helminth of the wood rat is *Böhmiella wilsoni* and it constitutes a new host record.

Trichuris muris, another new host record, infected 30 percent of the wood rats.

The only sexually mature cestode collected is a species in the genus *Andrya* but on the basis of material collected, it could not be classified to species.

The hepatic tissue of four wood rats contained cestode larvae, *Taenia taeniaeformis*, a new host record.

The ectoparasites collected were *Cuterebra* larvae, ticks and mites in the genera *Ixodes* and *Eutrombicula* respectively, and fleas in the family Dolichopsyllidae.

REFERENCES

BLAIR, W. FRANK 1939a—New mammals from Texas and Oklahoma, with remarks on the status of *Thomomys texensis* Bailey. Occas. Paers Mus. Zool. Univ. Mich. 403: 5-7.

———1939b—Faunal relationship and geographic distribution of mammals in Oklahoma. Amer. Midl. Nat. 12(1): 85-103.

CAHALANE, VICTOR H. 1947—Mammals of North America. Macmillan Co., pp. 487-500.

CHANDLER, ASA C. 1945—*Trichuris* species from California rodents. Jour. Parasit. 32(4): 284-286.

DIKMANS, G. 1935—New nematodes of the genus *Longistriata* in rodents. Jour. Wash. Acad. Sci. 25(2): 72-81.

GOLDMAN, EDWARD A. 1910—Revision of the wood rats of the genus *Neotoma*. North Amer. Fauna, No. 31, 107 pp.

HALL, M. C. 1916—Nematode parasites of mammals of the orders Rodentia, Lagomorpha, and Hyracoidea. Proc. U. S. Nat. Mus. 50: 1-258.

LUCKER, JOHN T. 1943—A new trichostrongylid nematode from the stomachs of American squirrels. Jour. Wash. Acad. Sci. 33(3): 75-79.

MERRIAM, C. HART 1894a—Abstract of a study of the American wood rats, with descriptions of fourteen new species and subspecies of the genus *Neotoma*. Proc. Biol Soc. Wash. 9: 117-128.

———1894b—A new subfamily of Murine rodents—The Neotominae—with description of a new genus and species and a synopsis of the known forms. Proc. Acad. Nat. Sci. Phila. 46: 225-254.

POOLE, EARL L. 1940—A life history sketch of the Allegheny wood rat. Jour. Mammal. 21(3): 249-270.

STILES, C. W. 1932—Helminthological notes. Soc. Proc. Helm. Soc. of Wash, Jour. Parasitol. 19: 90.

TINER, JACK D. 1948—Observations on the *Rictularia* (Nematoda: Thelaziidae) of North America. Trans. Amer. Micro. Soc. 67(2): 192-200.

TRAVASSOS, LAURO 1921—Contribuicoes para o conhecimento da fauna helmintolojica brasiliero. Ensaio monografico da familia Trichostrongylidae Leiper, 1909. Mem. Inst. Oswaldo Cruz 13: 5-125.

TUCKER, HAL 1942—*Nematodirus tortuosus* n. sp. (Nematoda) from the rat, *Neotoma*. Jour. Parasit. 28(2): 159-161.

VESTAL, ELDEN H. 1938—Biotic relations of the wood rat (*Neotoma fuscipes*) in the Berkeley Hills. Jour. Mammal. 19(1): 1-36.

VOGE, MARIETTA 1946—A new anoplocephalid cestode, *Andrya neotomae*, from the wood rat *Neotoma fuscipes*. Jour. Parasit. 32(1): 36-39.

VORHIES, CHARLES T. AND WALTER P. TAYLOR 1940—Life history and ecology of the white-throated wood rat, *Neotoma albigula albigula* Hartley, in relation to grazing in Arizona. Univ. Ariz. Agric. Exp. Sta. Tech. Bull. 86, 72 pp.

YORKE, W. AND P. A. MAPLESTONE 1926—The nematode parasites of vertebrates. P. Blakiston's Sons and Co., 584 pp.

Life History of the Water Shrew (Sorex palustris navigator)

Clinton H. Conaway*
616 N. Lake, Madison, Wisconsin

This contribution to the life history of the water shrew (*Sorex palustris navigator*) is based upon a combination of field and laboratory studies. Published literature relating to the species is largely confined to taxonomic or distributional considerations. Only a few incidental observations concerning the habits of this small semi-aquatic insectivore are recorded.

In the autumn of 1947 preliminary collection of specimens was begun. Subsequently it was indicated that sufficient material might be obtained to make a life history study possible. In February of 1948 a more detailed approach to the problem was started. This report is based upon material collected between September 1947 and September 1949. All specimens collected were obtained in western Montana, the majority being taken in Missoula County. This region is entirely within the range of the subspecies *Sorex palustris navigator* as defined by Jackson (1928).

Acknowledgments

During the course of the study valuable assistance was given by many individuals among the staff and students of Montana State University and the University Biological Station. I am particularly indebted to Dr. Philip L. Wright, under whose direction the study was conducted, and who gave counsel and assistance in all phases of this work. My wife spent many hours in the field and laboratory aiding in every way possible. I am also indebted to Dr. H. W. Mossman for helpful comments on the section concerned with reproduction.

Methods

Specimens were collected by the use of back breaker mouse traps baited with peanut butter to which sufficient anise oil had been added to give a pronounced odor. Animals were ordinarily brought into the laboratory and autopsied within a few hours after being removed from the traps. When this was not possible autopsies were done in the field. In all instances an attempt was made to obtain uniform conditions and materials. Thus, frozen specimens were allowed to thaw and wet specimens were dried before autopsy proceedings were begun. The same instruments were used in making all weights and measurements.

Animals were weighed and measured, then examined for ectoparasites. Following this the animal was skinned. The reproductive tract was removed from the body and preserved in Mossman's modification of formalin, alcohol,

* Parts of this work were included in a thesis submitted to the graduate faculty of Montana State University as partial fulfillment of the requirements for the degree of Master of Arts. The study was conducted at Montana State University and Montana State University Biological Station.

and acetic acid fixitive (Guyer, 1936). The stomach and intestines were removed and preserved in 10 per cent formalin. After a cursory examination of the skinned carcass for parasites or abnormalities, the head was removed and the remainder discarded. The skin was examined for skin glands, pigmentation, and molt, after which it was prepared as a study skin.

A total of 119 specimens was obtained during this study; of that number 35 were taken by other collectors. While most of these specimens were obtained by individuals collecting in company with me, others were taken by independent collectors. In the latter instance if specimens could not be given to me fresh they were preserved entire in 10 per cent formalin. Therefore, there is considerable variation in the extent and nature of the data available from various specimens. No body weights or measurements were taken on formalin preserved specimens. Some specimens were also partially eaten by planaria or damaged in other ways. In all instances only those data which could be obtained in a uniform manner were used for comparisons.

Details of special techniques are given in the sections relating to their use.

HABITAT

In reference to the habitat of *Sorex palustris*, Jackson (1928) states it is "seldom found at any great distance from water, which may be a lake or pond, a brook or merely a pothole in a swamp bog or forest." Borell and Ellis ((1934) remark that the water shrew prefers "slow moving streams with logs and drift" while Grinell and Storer (1924) and Long (1940) state it is found along swift streams.

The general range of this species is usually considered as the Canadian and Hudsonian zones (Dalquest, 1948). In western Montana the Canadian zone is a heavily timbered region, characterized by such tree species as Douglas fir[1] (*Pseudotsuga taxifolia*), grand fir (*Abies grandis*), western larch (*Larix occidentalis*) and lodge pole pine (*Pinus contorta*). Altitudinally this zone usually lies between 4000 and 6000 feet, although there is much local variation. Above the Canadian lies the Hudsonian or timberline zone. Here the dominant trees are white bark pine (*Pinus albicaulis*) and alpine fir (*Abies lasiocarpa*). A detailed discussion of the life zones in Glacier Park is given by Bailey (1918). While the water shrew ordinarily occurs at rather high elevations it has been recorded as low as 300 feet in western Washington along fast cold streams descending from nearby mountains (Jackson, 1928).

It was possible for me to examine the exact sites at which 101 of the 119 specimens were obtained. These specimens were all taken at elevations between 2900 and 6950 feet. All but a few were trapped along rapid streams. However, relatively few traps were set in other habitats since the objective of trapping was primarily to secure specimens. Consequently traps were set in those habitats which were most productive. As the study continued trapping techniques became more refined and habitats were carefully selected.

It became apparent that the majority of specimens were taken in rather limited habitats. These regions were along fast cold mountain streams having

1 Common and scientific names are according to Kelsey and Dayton (1942).

banks which offered favorable cover. Such banks were composed of large stones, boulders and tree roots forming many crevices and overhanging ledges (fig. 1). Many specimens were secured where streams flowed beneath such banks in the crevices or where small springs entered a larger stream under similar conditions. During the latter part of the study trapping was largely confined to streams presenting these physical characteristics.

Vegetation along such habitat was typically Canadian in composition. Mosses and liverworts occurred on the rocks near the water. Near the edge of the stream such plants as: green pyrola (*Pyrola chlorantha*), sidebell pyrola (*P. secunda*), red baneberry (*Actaca rubra*), and bearbearry (*Arctostaphylos uva-ursi*) frequently occurred. The chief tree species along good habitats was Douglas fir (*Pseudotsuga taxifolia*). Grand fir (*Abies grandis*) and Pacific yew (*Taxus brevifolia*) were present in some habitats.

When setting traps the method employed was to wade in the stream

Fig. 1.—Typical water shrew habitat along a small stream showing overhanging banks and crevices.

placing traps beneath the banks within a few inches of the water's edge. By working from the stream it was possible to select and trap in favorable sites which were not accessible from the bank. Traps were secured by a two or three foot length of No. 28 copper wire to prevent their loss if they fell into the stream. Ordinarily traps were placed 10 to 100 feet apart, depending on the available sites. All traps were numbered and the numbers recorded to facilitate recovery. Considerable care was used in placing the traps so that three or four hours were required to set 30 to 40 traps. Usually traps were set during an afternoon and recovered the next morning. Approximately one specimen for every 30 traps was obtained when trapping under optimum conditions.

Since the trapping was of a specialized nature, the results cannot be considered as a random sample. However, a listing of the various categories of habitats and the numbers of individuals obtained is at least indicative of some habitats of water shrews. Table 1 indicates the habitats of 101 shrews for which positive data are possessed (excluding the 18 specimens for which no precise habitat data are available) and the number of individuals caught in each type.

TABLE 1.—Habitats of specimens captured

Habitat	Number
Artificial stone walls	17
Log bridge abutments and retaining walls	7
Overhanging banks and crevices	56
Brush and logs at water's edge	10
Edge of dams and log jams	3
Water cress near bank	5
Stream in meadow	3

The artificial stone walls listed in Table 1 were located along the water's edge either as foundations of abandoned mine buildings or along the Rattlesnake River near Missoula where they had been constructed to prevent overflow (fig. 2). Water either flowed along the bases of such structures or higher varying with the stream conditions. The next category is essentially the same except that these structures were of log and loose rock (fig. 3). Overhanging banks and crevices are those natural situations previously described. Brush and logs include such sites as windfalls and other debris along the streams' edge (fig. 4). The three specimens taken at the edge of dams and log jams were all trapped where small flows of water seeped through these barriers. Five specimens were taken in traps placed on mats of water cress (*Rorippa nasturtium-aquaticum*) in shallow water just a few inches from a rocky bank. Of the three specimens secured in meadow conditions, the first was obtained at 3200 feet in elevation, about 30 feet from the mouth of a small stream only a few inches wide, which flowed through a grass meadow before entering the Rattlesnake River. The second specimen was taken at an elevation of 6000 feet in a run of *Microtus richardsoni*, along a small stream flowing through a subalpine meadow. Only a few hundred feet from this

Fig. 2.—Stone wall habitat. A specimen was trapped at point indicated by the arrow.

meadow the stream descended through an area closely resembling that which has been described as optimum trapping habitat. The third animal was trapped along a stream which meandered several hundred feet through a meadow and connected two small lakes.

All traps were placed within a few inches of water since preliminary trapping was most successful in such places. The greatest distance any specimen was taken away from water was seven inches. Rand (1944) records having taken a water shrew ten feet from the water's edge but most other records indicate specimens were taken nearer to water. Hall (1946) successfully trapped water shrews by using a modification of Stirton's (1944) method for trapping *Rheomys*. A barrier was placed across a stream and a trap placed in a depression in the center of the barrier. This method was not used in the present study since specimens were obtained readily by trapping along the banks.

AGE DETERMINATION

In order to understand the reproductive cycle and other phases of the life history of the water shrew it is necessary to have a method of approximating the age of the specimens obtained. Workers in the past have used several criteria to determine age within several species of shrews which have been studied. Pearson (1945) has adequately reviewed these various methods and concluded that such criteria as body weight, reproductive condition, scars on tail, and body length are not sufficiently accurate to use for determining age. Working with *Blarina* he developed a system for determining age based upon toothwear and the assumption that such attrition will be relatively constant throughout the animal's life. Toothwear had previously been used by other

Fig. 3.—Retaining wall. The arrow indicates the site where a specimen was trapped.

workers as an index to age in Insectivora. Jackson (1928) divided shrews into four age categories based on the amount of toothwear. Hamilton (1940) working with *Sorex fumeus* likewise used toothwear as an index of age, along with other criteria such as body weight and amount of hair on the tail. Eadie (1939) found that *Parascalops* collected in March and April could be classified into four well defined groups based upon toothwear. He considered these to be representative of one, two, three, and four year old classes.

Pearson (1945) arbitrarily selected seven representative specimens of *Blarina* chosen to show graded degrees of wear from very slight to extreme wear. These were assigned numbers from one to seven according to the extent

Fig. 4.—Debris at edge of stream. A specimen was trapped at the place indicated by the arrow.

of wear and all other skulls were compared with this series as a standard. Each skull compared was assigned a number corresponding to that of the standard with which it was most similar. The toothwear numbers were then plotted against the months of the year in which they were collected. When this was done a regression was obtained and it was apparent that two groups existed during the summer. That group showing a small amount of toothwear was considered to be the juvenile population, while the other group was considered to be the adult population, i.e., those having survived one winter.

Since Pearson's technique of comparison is rather subjective, it was decided to use a different technique for determining toothwear in this study. The method employed was to obtain a standard series of measurements of the length of a number of representative teeth in each specimen (fig. 5). The individual measurements were then totaled to obtain a toothwear number for each specimen.

For each specimen the following measurements were taken:

A. Right and left maxillary tooth rows.
   1. PM3—Distance from base of cingulum to tip of metacone.
   2. M1—Distance from base of cingulum to tip of metacone.
   3. M2—Distance from base of cingulum to tip of metacone.

B. Right and left mandibular tooth rows.
   1. I_1—Distance from base of cingulum to apex.
   2. C_1—Distance from cingulum to tip of protoconid.
   3. M_1—Distance from cingulum to tip of protoconid.
   4. M_2—Distance from cingulum to tip of protoconid.

All measurements were taken with a dissecting microscope and filar micrometer at a magnification of twenty-three diameters. To measure the maxillary teeth the skull was mounted upon a block and fixed in position to obtain a buccal view of the tooth row in a plane horizontal to the stage of the microscope. When one side had been measured the skull was then turned with the other tooth row up in a similar position and measured. The mandibles were separated and placed on the stage of the microscope and a buccal view thus obtained. The fourteen individual measurements were then added and the total plotted directly in occular units (fig. 6). Conversion from occular units to micra (one occular unit = 3.5 micra) was not computed since for the purpose of determining comparative figures this would be superfluous.

Although an attempt was made to standardize the technique, some variation would be expected. To determine the extent of this variation three skulls were each measured ten times and the standard deviation of each computed. The results of this were as follows: for sample one, the mean of ten trials was 4217 with a standard deviation of 23.7; for sample two, the mean was 4525 and the standard deviation, 31.6; and for sample three, the mean was 4945 and the standard deviation, 24.6. It may be seen from figure 6 that slight variations in measurements as indicated by standard deviations of this magnitude would probably not result in confusion between the two age classes of shrews recognizable during the summer.

Figure 6 represents the toothwear numbers plotted against the months in which the specimens were obtained. It may be seen that a very definite trend in toothwear exists with the highest numbers occurring in June and the lowest in August. The nature of this trend supports the hypothesis that toothwear is relatively constant through the course of the animal's life and that it is feasible to determine age by a method based upon toothwear. If it is assumed that this is so, it becomes apparent that in the population studied, the first young (those animals with the highest toothwear numbers) occurred in June and that the oldest specimens obtained were in their second summer.

Even though a well defined trend exists it will be noted that considerable spread occurs in the specimens of an age group during any month. This would be anticipated due to the variables involved. As has been previously pointed out, there was some variation in repeated measurements of the same skull and some error of measurement would be expected. In addition, individual variation in tooth length within the animals of the same age would be expected. Differential rates of toothwear undoubtedly account for considerable variation. As is indicated in figure 6, the breeding season is extended over a considerable period of time. This means that animals trapped on the same date may differ in age by several months even though they were born during the same breeding season.

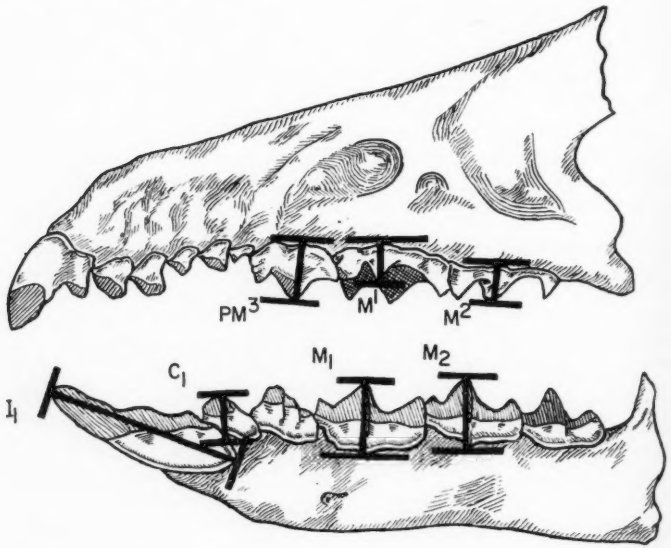


Fig. 5.—Lateral view of the anterior portion of a water shrew skull. The measurements taken to determine "tooth-wear number" are indicated by the lines connecting parallel bars.

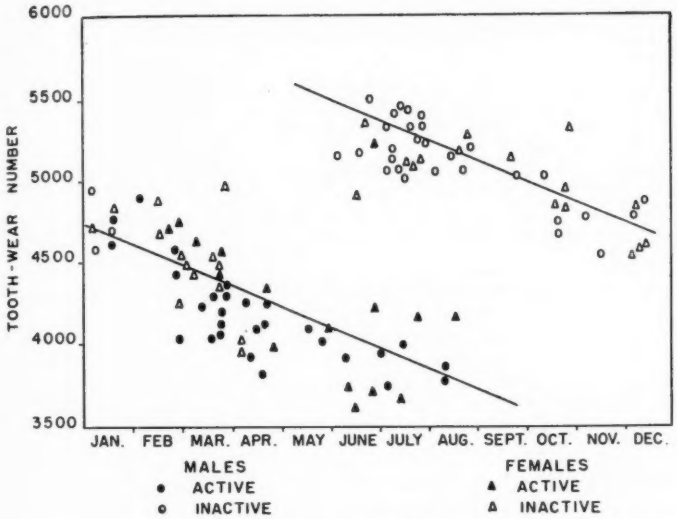


Fig. 6.—Age determination of water shrews by tooth-wear. Specimens with the lowest tooth-wear number are the oldest. Two age classes are seen to exist in the summer population. "Active" denotes males producing sperm or females pregnant and/or lactating.

In the following sections animals will be classed as old or young based upon their toothwear numbers. "Old" will arbitrarily be used to designate animals after January 1 of the first winter, while "young" will refer to animals not yet having reached January 1 of their first winter. The terms "mature" will refer to sexual maturity and "immature" to sexual immaturity.

WEIGHTS AND MEASUREMENTS

Although the weights of an individual shrew would be expected to vary considerably within short periods of time as Pearson (1945) has shown with *Blarina*, certain well defined trends can be seen in the body weights of male water shrews. An increase in the body weights of males occurs concomitantly with the onset of sexual activity. A similar increase associated with sexual activity has been reported in other members of the genus *Sorex*. In *Sorex fumeus* this occurs in March (Hamilton, 1940), in *Sorex araneus* in mid-March (Brambell, 1935), and early in April in *Sorex minutis* (Brambell and Hall, 1937).

Figure 7 indicates the body weights of all male specimens, their testicular condition, and the date of capture. In Table 2 the male animals obtained during November, December, and January are recorded with their body weights, testis weights and testis condition shown. From examination of these data it may

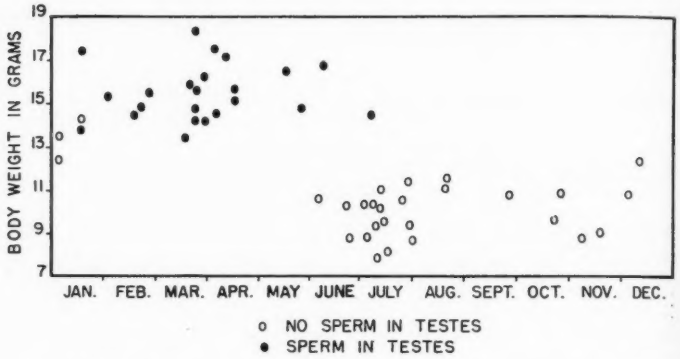


Fig. 7.—Body weights of male water shrews. All males not producing sperm during the summer are young animals, while all producing sperm are old.

be seen that the increase of body weight is closely associated with the increase of testicular weight and activity. The mean body weight of the twenty-five males whose testes contained sperm was 15.4 ± 1.3 gram,[2] while the mean body weight of twenty-two males whose testes were inactive was 9.7 ± 1.1 grams. When the two groups were subjected to the "t" test (Fisher, 1938) the difference in weight between them was found to be highly significant with P. being less than .01.

A comparison by the "t" test of the body weights of fifteen immature females with the weights of twenty-seven mature females (young or old animals having large follicles or pregnant and/or lactating) indicates there is a highly significant difference between the two groups since P. is less than .01. The mean body weight of the immature females was 9.7 ± .6 while that of the mature females was 12.3 ± 1.6. Figure 8 shows that while young shrews are lighter than old individuals this character is not consistent or definite enough to make weight a criterion for age determination.

When the mean body weight of immature females was compared with that of immature males by the "t" test it was found that there was no significant difference, P. being greater than .05. However, there is a highly significant difference between the mean weight of mature males as compared to mature females. In this instance P. is less than .01.

For a comparison of the body measurements of the two sexes those young specimens taken before October were eliminated since some were obviously not fully grown. Of thirty-eight males taken after October the mean body measurements were as follows: total length 153.4 ± 5.4 mm., tail length 73.0±3.7 mm., hind foot 19.9±.5 mm. The measurements of thirty-nine females during the same period are: total length 149.4 ± 5.2 mm., tail length

[2] Standard deviation is given following the symbol ± unless otherwise noted.

72.1 ± 3.4 mm., hind foot 19.8 ± .5 mm. When the measurements of the males were compared with those of females by the "t" test, no significant difference was found between the tail or foot lengths. A slight, but highly significant difference exists between total lengths.

REPRODUCTION

The reproductive cycle of the water shrew was studied by analysis of reproductive tracts from trapped specimens. The entire tract of both sexes was removed at autopsy and preserved in A. F. A. In addition, mammary tissue from many females was preserved. After fixing, tissues were stored in 70 per cent alcohol.

Before sectioning, the testes were weighed. They were prepared for weighing by removing the epididymis and all connective tissue outside the tunica albuginea. Each pair was then removed from the alcohol in which they had been stored for a month or more and dried by rolling on a paper towel for a few seconds. They were next placed in a capsule which had been weighed just previously. Both capsule and testes were weighed and the weight of the testes obtained by subtracting the weight of the capsule from the combined weight of testes and capsule. All weights were taken on a Roller Smith precision spring balance. In order to obtain some comprehension of the magnitude of error which could be expected in this method of weighing, one pair of testes was weighed repeatedly during several days. After each weighing these testes were returned to alcohol for not less than one hour before another weight was obtained. The mean for twelve repeated weights of one pair of mature testes was 112.4 ± .8 mg. The mean for twelve repeated weights of one pair of immature testes was 1.1 ± .1 mg.

The small standard deviations show that slight variation is obtained in repeated weighings, thus the method is sufficiently accurate for comparisons of the weights of fixed testes. Although weights of fixed organs may not be as desirable as either desiccated or fresh weights, they adequately indicate the gross changes in testicular weight which occur during the growth and reproductive cycle.

Histological preparations were made of the gonads of both sexes. Sections of one testis and the tail of an epididymis were prepared from each male. The female tracts were usually separated at the cervix and each uterine horn and attached oviduct and ovary was then serially sectioned. Mammary tissue from many mature animals was also sectioned. The dioxane method was used for all material. Sections were cut at 10 micra and stained with Ehrlich's hematoxylin and eosin.

REPRODUCTION IN THE MALE

A total of 61 male reproductive tracts was studied. The material represents specimens collected in all months of the year.

From figure 6 it may be seen that all males taken during the summer and autumn, which were classified as young by their toothwear, had inactive testes.

In contrast, those taken in the same period and classified as old were in active spermatogenesis. Figure 9 shows the testicular weights and spermatogenic states of all specimens. Between May, when the first young male was taken, and November all young animals present an essentially uniform condition. The testicular weights of immature animals during this period varied from .4 mg. to 4.0 mg. for both testes. Microscopically the testes were similar; the seminiferous tubules were solid with only spermatogonia and sertoli cells being present. A specimen taken December 5, 1948 shows the first indication of sexual activity. The testes of this immature individual weighed 10.8 mg. and many mitoses were apparent in the seminiferous tubules. Another immature specimen taken December 6, 1947 whose testes weighed 64.8 mg. showed many spermatids in the seminiferous tubules. No sperm were present in either the testes or epididymides of this animal. The data from these and additional specimens taken during January are summarized in Table 2.

TABLE 2.—Onset of sexual activity in the male

Date	Body weight	Testis weight	Testis condition
November 7, 1948	8.6 gm.	2.2 mg.	inactive
November 14, 1948	8.9 gm.	1.6 mg.	inactive
December 5, 1948	10.6 gm.	10.8 mg.	many mitoses
December 6, 1947	12.0 gm.	64.8 mg.	spermatids
January 4, 1948	12.0 gm.	30.4 mg.	many mitoses
January 24, 1948	13.2 gm.	68.8 mg.	spermatids
January 24, 1948	13.4 gm.	132.2 mg.	sperm
January 24, 1948	17.4 gm.	170.8 mg.	sperm
January 24, 1948	13.9 gm.	95.8 mg.	spermatids

All old specimens taken after the beginning of February possessed testes weighing above 110 mg. with both testes and epididymides containing sperm. No evidence of testicular regression was found in any of the material. Two old specimens taken during mid-August are in active spermatogenesis with no indication of regression. Since no old specimens were taken after this date, the question of possible regression is still unanswered. In *Sorex araneus*, Brambell (1935) found no positive evidence of regression. Likewise Hamilton (1940) in the study of *Sorex fumeus* found no indication of regression in the males, his last male specimen being taken in early September. However, Pearson (1944) obtained specimens of *Blarina* in the autumn in which the testes were regressing.

The general pattern of the male reproductive cycle in *Sorex palustris* is similar to that of other Soricidae as indicated from published studies. The most striking peculiarity is in the earliness of the season of onset of spermatogenesis. As previously shown, the first activity in immatures was noted early in December and all old specimens taken after the beginning of February were in active spermatogenesis. In *Sorex araneus* sperm appears in testes in the second half of March (Brambell, 1935), while in *Sorex minutis* the earliest

appearance was recorded on March 31 (Brambell and Hall, 1937). For *Sorex fumeus* the time is given as the latter part of March (Hamilton, 1940). *Blarina brevicauda* first showed testicular growth in late January and sperm appeared by the end of February (Pearson, 1944).

Considerable individual variation in testicular condition was found in water shrews taken the same day and in the same area. Also, although the first evidence of testicular activity was seen in early December, a specimen secured in late January was not yet producing sperm. These facts, together with the number of specimens showing intermediate stages of development during the period of rising testicular activity, are suggestive that development occurs rather slowly and with considerable individual variation. Hamilton (1940) indicates that in *Sorex fumeus* this process is very abrupt and uniform in the population since in mid-March animals were inactive while by early April all specimens were mature.

From the material examined it seems that no breeding occurs in young males during their first summer since during this time the testes are of small size and undeveloped. In December and January spermatogenesis begins. At this time there is a marked increase in testicular weight. Spermatogenesis continues throughout the second summer until at least August when the last old specimen was obtained.

REPRODUCTION IN THE FEMALE

The study of the female cycle is based upon analysis of the reproductive tracts from fifty-eight specimens. No attempt is made here to describe in detail the microscopic anatomy of the reproductive tracts; only those features which are essential to an understanding of the events of the cycle are included. The number of specimens available for study is inadequate to clarify certain details of the cycle and some data are subject to various interpretations.

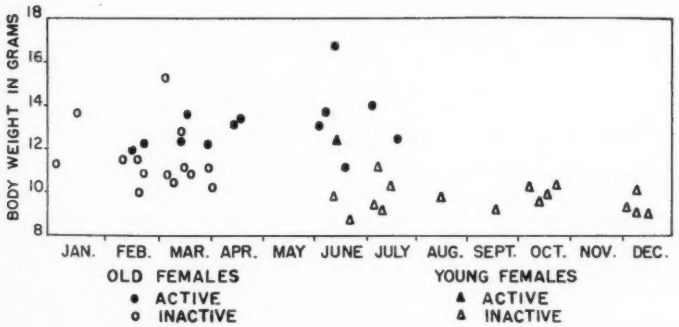


Fig. 8.—Body weights of female water shrews. There is no clear separation between the weights, of old and young animals. "Active" indicates pregnant and/or lactating females.

Reproductive tracts characterized by small ovaries without large follicles or corpora lutea are termed "inactive" as opposed to those with large follicles or corpora which are called "active." Large follicles without antra are termed maturing follicles. The term Graafian follicles is used to refer to only those follicles in which antra are present.

The inactive tract.—With the exception of three young females taken in June, all of the young specimens obtained during the summer and fall (twenty-six individuals) belong to this class. These reproductive tracts are inconspicuous and somewhat difficult to locate at autopsy. Microscopically the ovaries are small dense masses of tissue composed chiefly of stroma and primary follicles. The uteri of inactive water shrews are thin-walled with inconspicuous glands. The entire picture is one of reproductive quiescence.

The onset of reproductive activity.—The earliest indication of rising ovarian activity is seen in a specimen obtained January 4. The ovaries of this individual appear slightly larger than those of animals taken in early December and also contain a few maturing follicles. In a specimen obtained January 24 both ovaries are greatly enlarged with numerous maturing follicles. All old females taken between this date and August, when the last individual was secured, are in various stages of reproductive activity. Fourteen specimens collected between January 25 and Aril 2, although they are not pregnant, show considerable development of the reproductive tract. The uteri are enlarged, and there is considerable glandular proliferation. The ovaries are large and contain numerous maturing or Graafian follicles, but ovulation has not occurred. Sperm is present in the oviducts and periovarian spaces of two individuals from this period (Table 3, group I). The ovaries of these two specimens are highly vascular, and there are many large Graafian follicles. The absence of corpora lutea in any of the ovaries from these 14 non-pregnant, but apparently estrus or near estrus, animals indicates that ovulation is induced only by copulation in the water shrews. If ovulation were spontaneous, it seems probable that corpora lutea of the estrous cycle would be found in some of the non-pregnant animals. In all Soricidae in which the manner of ovulation is recorded it has been found to occur only upon the stimulus of copulation. Pearson (1944) demonstrated that repeated copulation was necessary to induce ovulation in *Blarina*. Indirect evidence indicates that in *Sorex araneus* ovulation is also induced by copulation (Brambell, 1935).

During the period between January 25 and April 2, five of the specimens collected are either pregnant or post partum (Table 3). One pregnant animal was obtained as early as February 24. Thus, while some of the females collected during the early months of the breeding season have not yet ovulated, others are pregnant or parous. This suggests that the females of the population arrive at estrus over a period of several months since the males are fully mature during the whole period and would presumably breed when the females were receptive. In three separate instances pre-ovulatory females were taken in one trap and a male taken at the same time in another trap less than ten feet away.

Atretic follicles are not common in the ovaries of pre-ovulatory animals. The final maturation of follicles seems to be slow, occurring in different individuals at variable times.

First pregnancy.—Since the post partum phase of the cycle presents certain peculiarities, it is advisable to discuss the first pregnancy separately from subsequent events in the cycle. From the available material the most useful

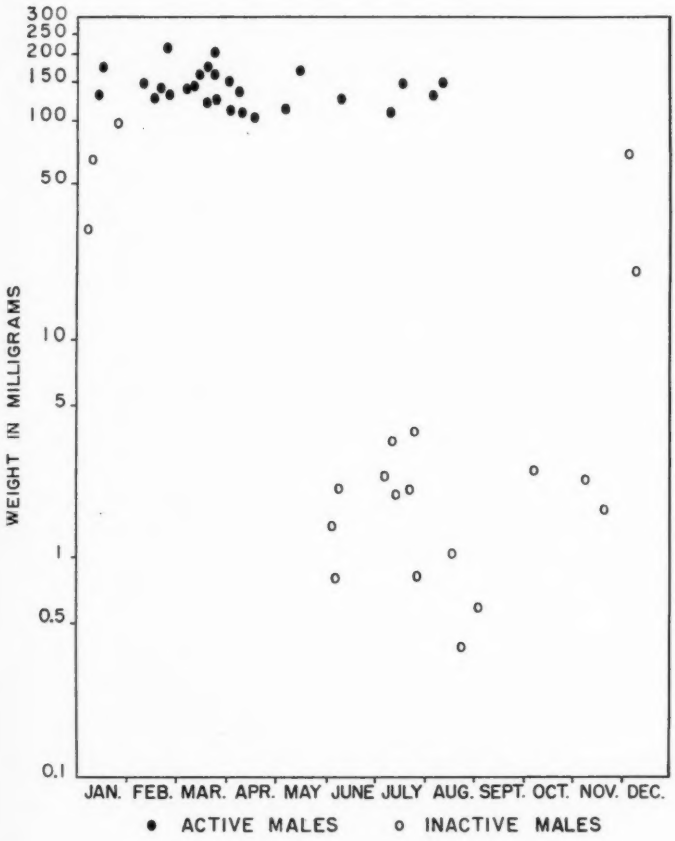


Fig. 9.—Testicular weights of male water shrews (semi-logarithmic scale). Active denotes sperm in the testes.

single criterion in determining whether an animal is nulliparous or recently parous is the degree of mammary proliferation. Animals early in their first pregnancy exhibit little differentiation of mammary tissue with absence of the lobule-alveolar development characteristic of those animals which are recently parous. Although both endometria and myometria of the uteri from animals in the first pregnancy appear less highly developed than in uteri from animals which are in a subsequent pregnancy, no precise character to differentiate the two classes was found. Brambell (1935) found in *Sorex araneus* a fibrous connective tissue stratum was present between the mucosa and muscularis of the nonparous uterus and this disappeared following pregnancy. No similar structure is seen in the water shrew.

From analysis of the corpora lutea of four animals considered to be in their first pregnancy (table 3, group II) it is possible to trace a portion of the cycle of the corpus luteum. It is of advantage to use, when possible, those specimens that are in their first pregnancy, since confusion of corpora of previous ovulations with corpora of pregnancy is less likely. Additional selected pregnant specimens (table 3, Nos. 152, 214, 740) in which accurate matching of corpora and embryos seems possible, have been used to understand more clearly the cycle of the corpus.

Corpora in the two multiparous specimens with tubal embryos (Nos. 152 and 214) are not fuliy developed; antra are still present and the average diameter is .40 mm. in one and .45 mm. in the other. Those animals in their first pregnancy which have free uterine blastocysts (Nos. 685 and 688) exhibit large corpora of approximately .50 mm. diameter. These corpora have no antra and the luteal cells are large. The corpora of a specimen containing implanted neural crest embryos (No. 680) average .50 mm. in diameter while those of the female with limb bud embryos (No. 165) average .62 mm. in diameter. Corpora from an animal with near term fetuses (No. 740) show marked regressive changes both in gross size and in cell structure. The size of these corpora is .44 mm. average diameter, the lutein cell nuclei are somewhat pyknotic, and connective tissue infiltration is apparent. The maximum size of the corpus appears to be reached at about the time the embryos are in the early limb bud stage.

From the material studied it seems that the corpus of the water shrew closely resembles that of *Blarina* in corresponding phases of pregnancy (Pearson, 1944). The marked regression of the corpora in the specimen with near term fetuses indicate that regression of the corpora would be expected at about the time of parturition or shortly after as has been reported by Pearson (1944) in *Blarina* and in *Sorex araneus* by Brambell (1935).

Post partum.—Eight specimens (Table 3, group III) are believed to be animals that had recently borne young and were lactating at the time of capture. Histological examination of mammary tissue from these individuals indicates varying degrees of lactation activity. From the analysis of the reproductive tracts of this group of animals it appears that the post partum phase

of the cycle is rather complex and that a clear understanding is impossible from the material available for study.

Three post partum animals are actively lactating and pregnant indicating that a post partum ovulation has occurred. The ovaries of female No. 152 (table 3) have two sets of corpora lutea. One set is degenerating and is considered to be the corpora of the past pregnancy. A second group of corpora have antra present and are very recent. Embryos in the pronuclear stage are present in the oviducts. The placental sites of the past pregnancy are very conspicuous and repair of the endometrium is incomplete in these regions. This specimen can be no more than a few days post partum. A second lactating specimen (No. 217) has large active corpora and unimplanted blastocysts in the uterus. The corpora of the past pregnancy have completely degenerated. Repair of the endometrium is complete although placental sites are still conspicuous. The third lactating post partum animal (No. 209) has implanted neural crest embryos. Only one set of corpora appear in the ovaries.

Four post partum animals in various stages of lactation activity have large corpora lutea but no embryos are present in the reproductive tracts. The corpora correspond to those of early implantation stages as previously described. Since the corpus in late pregnancy undergoes marked degeneration and has disappeared in all but one of the pregnant post partum animals, it seems that these corpora have resulted from a post partum ovulation. Numerous hypotheses may be advanced to explain the absence of embryos in these animals. Some of the most probable are: (a) unimplanted blastocysts were lost in preparation of tissue, (b) embryos were formed but degenerated because of poor preservation as a result of delayed fixation of tissues, (c) the post partum ovulation was spontaneous and there was no fertilization, (d) the post partum ovulation was induced by matings but fertilization did not occur, (e) embryos were formed but degenerated from natural causes.

In examination of each of the above mentioned hypotheses some may be eliminated with relative certainty. That all blastocysts were lost in histological preparation in only these tracts but retained in other is improbable. Equally remote is the probability that embryos had autolysed between the animal's death and fixation of the tracts since in other specimens subjected to the same conditions blastocysts were in good preservation. Also the maternal tissue in the questionable specimens was well preserved. The evidence from first pregnancies indicates that ovulation is induced, so it is doubtful that post partum ovulations would be spontaneous. It is relatively improbable that sterile matings without fertilization would occur with high frequency, so it seems that this possibility would be subject to considerable doubt although it can not be disregarded.

The last remaining possibility, that embryos were formed but degenerated at some stage in development, seems to be the most probable conclusion. In the four uteri implantation sites are visible. These may be either placental scars from the litter being suckled or the site of resorbed embryos. No recog-

nizable degenerating embryos were found. If degeneration of embryos had occurred it was advanced to a stage where there was no definitely recognizable embryonic tissue. An amorphous debris in several of the uterine lumina is similar to that found in the rabbit during resorption (Hammond and Marshall, 1925) and may represent advanced degeneration. If degeneration were to occur at a very early stage little debris would be expected. It should be noted that the three lactating pregnant animals had embryos in rather early developmental stages and degeneration might have occurred later in these animals. Thus it is impossible to determine whether or not post partum pregnancies are ever successful in the water shrew.

Resorption of embryos and prenatal mortality has been studied in some groups other than the Soricidae. Hammond and Marshall (1925) found that if the domestic rabbit becomes pregnant in a post partum heat and the doe is nursing more than three or four young, the embryos usually die in the blastocyst stage. In extensive studies with the wild rabbit, *Oryctolagus cuniculus*, Brambell (1948) found no such increase in prenatal mortality rates of the litters during lactation. The rate of litter mortality in all pregnancies, however, was not less than 35 per cent with the peak of loss resulting from resorption occurring shortly after implantation. Work with the mouse, *Mus musculus* indicates that in this species foetal mortality is somewhat higher during lactation than in pregnancies not accompanied by lactation (Parks, 1923).

The final post partum animal to be considered (No. 214) is one in which the mammary tissue shows marked regression indicating that lactation activity is almost terminated. Two sets of corpora are present in the ovaries and four cell embryos are seen in the oviducts. The specimen apparently is similar to those preceding in that a post partum ovulation occurred but pregnancy did not result or was not maintained. The degenerating corpora are interpreted as those of the post partum ovulation. Another ovulation has occurred at the end of lactation, resulting in the embryos and fresh corpora.

Apparently all lactating specimens have experienced a post partum ovulation. Whether this is induced by copulation or is spontaneous is not known. At least some animals became pregnant as a result of the post partum ovulation. The possibility exists that these pregnancies might later be terminated by resorption. More than half of the post partum animals examined were not pregnant. The explanation of this is not known, but it appears that degeneration of embryos during lactation is a possible answer. Certain of these aspects of the post partum cycle are unique among the Soricidae which have been studied so far. In *Sorex araneus* a post partum heat is accompanied by a normal pregnancy which extends to term (Brambell, 1935). A similar situation exists in *Sorex minutis* (Brambell and Hall, 1937). *Blarina* has no post partum heat (Pearson, 1944).

Three specimens are listed as unclassified in group IV of Table 3. These specimens are old animals, but there is some doubt as to the interpretation of the data from them. Mammary tissue was not preserved from specimens

Nos. 180 and 110. For this reason no attempt has been made to analyze the data from these specimens. Animal No. 740 is pregnant and very close to term. The mammary tissue is well developed and apparently secreting, as would be expected in a term animal. It is impossible to determine whether or not the specimen was suckling a litter or had previously borne young.

Although details of the cycle in adult females are open to question because of the limited number of specimens studied, some of the gross aspects are more clearly apparent. All females taken between April 2 and August (when the last adult was secured) were pregnant and/or lactating. While the duration of the period of gestation and subsequent lactation is unknown, it seems probable the total time would not exceed two and one-half months. The duration of the combined period of pregnancy and lactation is about two months in *Blarina* (Pearson, 1944). Thus, probably at least two or three litters are produced by adult female water shrews during the breeding season.

Only four females were collected in which implanted embryos were found. Three of these contained six embryos and the fourth had five. In 12 records from various sources (Long, 1940; Grinnell and Storer, 1924; Borell and Ellis, 1934; Jackson, 1920; Hall, 1946; Warren, 1942) from five to eight embryos have been recorded with six being the most common number.

Transfer of blastocysts between uterine horns is indicated in specimen No. 680 since the distribution of corpora is one in the right ovary and five in the left, while three embryos occur in each uterine horn. As Brambell (1935) found in *Sorex araneus* and Pearson (1944) in *Blarina*, the water shrew ovary is encapsulated thus the mode of blastocyst transfer must be across the superior end of the cervix.

Reproduction in young females.—Three young females (table 3, group V) as previously indicated are in various stages of reproductive activity. The remainder of the young females are inactive. The reproductively active specimens were all obtained in June. Two of these animals have small tracts but both ovaries contain maturing follicles and the uteri are more developed than those from inactive tracts.

The third specimen taken on June 25 is pregnant. Four corpora appear in the ovaries and one unimplanted blastocyst is present in the uterus. Mammary tissue is abundant, but the lobule-alveolar system is undifferentiated. The animal appears to be in its first pregnancy. The presence of only four corpora and one blastocyst indicates this pregnancy may be somewhat atypical.

With the collection of additional spring and early summer specimens the significance and extent of reproductive activity in young females may be more accurately determined. It would seem, however, that breeding or at least successful pregnancy may be rather uncommon, since young animals taken later in the season are all inactive. Brambell (1935) found young *Sorex araneus* to be non-breeders. Pearson (1944) found evidence of breeding in early born young *Blarina* females. This may be the normal situation in *Sorex palustris* also, but it seems more probable that the precocious sexual activity rather rarely culminates in successful pregnancy.

TABLE 3.--Reproduction in the female*

No.	Date	Ovary	Uterus and Oviduct	Mammary Gland
	GROUP I.	Estrous		
150	Mar 13, '49	Graafian follicles (.30 mm. dia.)	sperm in oviduct	undifferentiated
159	Mar 20, '49	Graafian follicles (.37 mm. dia.)	sperm in oviduct	undifferentiated
	GROUP II.	First Pregnancy		
680	Feb 24, '48	6 (1, 5) C.L. (.50 mm. dia.)	6 (3, 3) embryos: neural crest stage	undifferentiated
685	Feb 29, '48	6 (4, 2) C.L. (.50 mm. dia.)	5 (4, 1) blastocysts: 1 (0, 1) degenerating ovum	undifferentiated
688	Mar 20, '48	11 (6, 5) C.L. (.49 mm. dia.)	5 (4, 1) blastocysts	undifferentiated
165	Apr 1, '49	5 (2, 3) C.L. (.62 mm. dia.)	5 (2, 3) embryos: limb bud stage	undifferentiated
	GROUP III.	Post Partum		
152	Mar 19, '48	6 (5, 1) new C.L. (.40 mm. dia.) 5 (3, 2) old C.L. (.33 mm. dia.)	6 (5, 1) tubal embryos: pronucleus stage 5 (3, 2) placental scars	actively lactating
217	Jun. 12, '49	12 (9, 5) C.L. (.55 mm. dia.)	8 (4, 4) blastocysts: placental scars	actively lactating
209	May 29, '49	14 (6, 8) C.L. (.63 mm. dia.)	6 (3, 3) neural crest embryos	actively lactating
122	Aug 13, '48	12 (8, 4) C.L. (.50 mm. dia.)	placental scars	actively lactating
74	Jul. 13, '48	9 (5, 4) C.L. (.55 mm. dia.)	placental scars	actively lactating
181	Apr 24, '49	5 (2, 3) C.L. (.60 mm. dia.)	placental scars	regressing
221	Jun. 27, '49	11 (7, 4) C.L. (.60 mm. dia.)	placental scars	regressing
214	Jun. 5, '49	5 (2, 3) new C.L. (.45 mm. dia.) 10 (4, 6) old C.L. (.38 mm. dia.	5 (2, 3) 4-cell stage embryos in oviduct 8 (4, 4) placental scars	regressing and non-secretory
	GROUP IV.	Unclassified		
180	Apr 17, '49	13 (3, 10) C.L. (.52 mm. dia.)	5 (2, 3) blastocysts: 6 (5, 1) unfertilized tubal ova: old placental scars	not preserved
740	Jun. 25, '48	12 (7, 5) C.L. (.44 mm. dia.)	5 (3, 3) near term embryos	well differentiated
110	Jul. 27, '48	6 (1, 5) new C.L. (.50 mm. dia.) 11 (5, 6) old C.L. (.28 mm. dia.)	5 (0, 5) blastocysts old placental scars	not preserved
	GROUP V.	Young Females		
218	Jun. 18, '49	few maturing follicles		undifferentiated
735	Jun. 19, '48	maturing follicles		undifferentiated
743	Jun. 25, '48	4 (1, 3) C.L.	1 (0, 1) blastocysts	undifferentiated

* Embryo, placental scar, and corpus luteum numbers are indicated with the total followed by the number in the right side and the number in the left side of the tract in parentheses. C.L. = Corpus Luteum.

FOOD HABITS

The stomach contents of 87 water shrews were analyzed in an effort to obtain some knowledge of the food habits of the species. The contents of these stomachs were chiefly a mass of finely divided food particles and fragments of chitin. All stomachs examined contained some material, the amount varying considerably in individual stomachs.

To prepare the stomach contents for study each stomach was removed from the formalin in which it was preserved, opened, and the contents placed in a vial. Dioxan was added to the vial and this mixture was vigorously agitated to separate all particles. After the particles were dehydrated, the dioxan was decanted away and the stomach contents mounted in Canada balsam. The particles were then examined under a binocular microscope at magnifications of 9, 18, and 27 powers.

Since the material was in a finely divided and fragmented condition it seemed impossible to obtain any reliable quantitative data. Therefore, all material which could be identified in each stomach was listed and the number of stomachs in which each class of food appeared computed to obtain the frequency of occurrence. Insect remains could be recognized by wings, fragments of appendages, tracheal tubes and fragments of exoskeleton. However, recognition of the order of insects represented was in many cases impossible. A reference collection of common insects was prepared and used for study and comparison in an effort to identify the remains of aquatic forms. Identification of fragments from immature aquatic insects was based upon the occurrence of characteristic gills and appendages.

The results of the analysis of stomach contents are tabulated in Table 4. Undoubtedly, certain classes of food items were completely or frequently overlooked. The results do, however, provide at least an indication of some foods of the water shrew.

It is apparent that the water shrew is primarily insectivorous. The high frequency with which aquatic organisms are encountered (49 per cent of the stomachs) is of interest since it indicates that a considerable portion of the food is obtained in the water. This would seem to be expected in a form which is highly specialized for aquatic existence as is the water shrew, but Hamilton (1930) in a study of thirteen stomachs of *Sorex palustris albibarbis* found aquatic organisms in only three stomachs and concluded that food was obtained largely from land. By bulk he found these stomachs to contain 78 per cent insect material, 4.4 per cent planaria, 3.1 per cent plant and 13 per cent undetermined.

Mammalian hair and skin appeared in three stomachs and in each case this was identified as shrew hair. In one instance the specimen containing shrew hair was taken about ten feet from a second partially eaten water shrew. In the other two stomachs there was no evidence to indicate the species of shrew from which the hair came.

Three individuals had apparently been feeding upon fish. Small fish

scales occurred in one stomach. Whether this material represented carrion or a fish taken as prey could not be determined. A second specimen when trapped held in its mouth the pectoral fins of a trout which had undoubtedly been cut off by a fisherman and cast aside. A third specimen with a small fish four cm. long in its mouth was taken at the edge of a shallow pool in which similar fish were found.

Although vegetable material was found in nineteen stomachs, it made up a very small proportion of the contents in each instance. It seems probable that much of this may have been ingested inadvertently during the course of feeding on other material.

From the study of food habits as shown by stomach contents it appears that insects are the most important food of the water shrew. It is also apparent that larvae of aquatic insects are taken very frequently. Experiments with a captive water shrew demonstrated that the animal was capable of taking small fish in an aquarium with ease. Under these artificial conditions, however, the fish were probably more easily taken than under natural conditions. One account of a water shrew capturing a small fish under natural conditions has been published (Lanpman, 1947). Therefore, it would seem that while the water shrew may occasionally take small fish they do not constitute an important food source.

PARASITES

Relatively few ectoparasites were collected from the 119 water shrews examined. Undoubtedly many ectoparasites left the dead shrews before they were removed from the traps; thus the small number of ectoparasites collected is not an index of host infestation. Two species of fleas were recorded. A total of four individuals of *Nearctopsylla hyrtaci* (Roths) were taken from three water shrews. A single specimen of *Corrodopsylla c. curvata* (Roths.) was obtained from another water shrew. The occurrence of *Nearctopsylla hyrtaci* represents the first United States record for this species which previously had been recorded from a variety of hosts in British Columbia (Kohls, 1950). Mites of the genus *Hirstionyssus* were found on two shrews while *Euphaemogamasus liponyssoides* (Ewing) was taken from another and *Euphaemogamasus nidi* (Michael) from a fourth specimen. A single unidentified nymphal tick was also recorded.

A total of four species of *Nematoda* were recorded from the water shrews examined. Larval Nematoda of the genus *Porrocaecum* occurred in the subcutaneous fascia of eleven specimens. These nematodes represented two species since both *P. americanum* Schwartz and *P. encapsulatum* Schwartz were identified. The parasites which occurred with the greatest frequency were two nematodes of the genus *Capillaria*. *Capillaria rauschi* Read was found in the stomachs of 43 per cent of 62 shrews for which this data was recorded. A second capillarid of an apparently undescribed species was found in the urinary bladder of 29 per cent of 62 specimens.

Cestode parasites were seen in only three of the 116 specimens examined. Two species of cestodes of the genus *Hymenolepis* were found in the duo-

denum of two animals. Identification to species could not be made on these forms since they were poorly preserved. Plerocerci of the genus *Tetrathyridium* were found in the coelomic cavity of a single specimen.

Identifications of the siphonaptera were made by W. L. Jellison and G. M. Kohls. The mites were identified by E. W. Jameson and H. L. Keegan. Determination of the nematodes was made by M. L. Kuns and W. Coil identified the cestodes.

DERMAL GLANDS

Sexually active male water shrews possess dermal glands located in the skin on each side of the body midway between the fore and hind legs. Only the sexually active males have such glands. This seems to be a unique situation since in all other species of Soricidae in which skin glands have been noted (with the possible exception of *Sorex cinereus*), they occur in both sexes, although they may be less prominent in the females (Pearson, 1946). Side glands were not visible in sexually immature male water shrews. They were first noted in a specimen collected December 6, whose testes weighed 64.8 mg. However, in a male collected December 5, whose testes weighed 10.8 mg., the glands could not be detected. In those animals obtained during January, which has testes weighing less than 100 mg., side glands were observable but not prominent. In all animals in full spermatogenesis the glands were very prominent both externally and internally on the skin. When the glands became fully developed, short white hair grew from them, thus producing an oval patch of white hair on the animals' sides, approximately eight mm. long. This hair was oily in appearance and matted together.

MOLT

The molts of the water shrew have been briefly discussed by Jackson (1928). He describes two molts, one occurring in the spring and the other in the early autumn or late summer. From the limited number of spring specimens available to him he concluded that the spring molt occurred in May or June. The fall molt usually occurred in August or September according to his description. Since a series of specimens from all months of the year were available in the present study, it has been possible to follow the molts more closely. The general progression of the spring molt is from anterior to posterior. Summer pelage is usually first evident on the rostrum. At this early stage molt seems to progress slowly as the data in Table 5 suggests. It will be noted that a large number of specimens secured during the late winter and spring show molt only on the rostrum, while few specimens are in more advanced stages of molt. The latest specimen showing spring molt was obtained May 31.

Frequently, although summer hair is apparent on the rostrum, pigmentation of the skin in other areas indicated hair proliferation had begun. Such pigmentation patterns seen on the fresh skin were highly irregular and frequently appeared as many small black spots each a few millimeters in diam

eter. These were distributed irregularly over the body. In some specimens in which the rostrum has molted no skin pigmentation was observed.

Two specimens taken in late April and three in May show advanced stages of molt. In these animals new summer hair covers the entire anterior parts of the body. All adults taken from June until mid-July are in complete summer pelage. It seems that while the rostrum and head may molt very early in the season the progress of molt is very slow at that time. During April or May the rate of molting increases so that by June it is completed.

The autumn molt occurs chiefly during late July and August. The pattern of this molt seems to be similar in both young and old animals. Table 6 summarizes data on this molt in both young and old specimens. The fall molt seems to represent the first molt of the young animals. Growth of new winter hair begins on the flanks or mid-dorsal region and spreads from this center. A second center of hair growth is seen to develop on the rostrum of some specimens. In such instances the last region to molt is an area over the back of the cranium. Examination of *Sorex palustris* specimens in the Fish and Wildlife collections and in the National Museum collections indicates that the preceding description in general applies to the fall molt although considerable variation in the region of the back where molt first begins is evident.

TABLE 4.—Analysis of eighty-seven stomachs

Food class	Number of stomachs	Percentage of occurrences
Insect	86	98.8
Tipulidae larva	5	5.7
Aquatic insect (immature)	43	49.4
Plecoptera naiad	12	13.8
Trichoptera larva	28	32.2
Ephemerida naiad	12	13.8
Simuliidae larva	1	1.1
Chironomidae larva	3	3.4
Arachnida	1	1.1
Oligochaeta	5	5.8
Sorex hair	3	3.4
Fish scales	1	1.1
Vegetable matter	19	21.8

Dalquest (1944), in a study of molting in *Sorex vagrans*, found that the spring molt occurred between March and May with a high degree of individual variability as to the time when it began. This molt was first evident between the shoulders and spread from that area over the body. The autumn molt occurred in October beginning on the rump, and later a second center developed on the nose as in the water shrew. An anomalous molt during mid-summer in which the summer pelage was replaced by a new summer pelage was noted in three specimens.

The molts of the water shrew are very similar to those of *Sorex vagrans*. However, in the water shrew the spring molt begins on the rostrum rather than on the shoulders. Considerable irregularity as to the time of occurrence of this molt in both species is apparent. The mode of progression of the autumn molt is similar in both *Sorex vagrans* and *Sorex palustris* although the months of occurrence differ. In the water shrews no indication of an anomalous mid-summer molt was seen.

TABLE 5.—Spring molt

Period	No. of specimens	Condition of molt
January 1-15	3	3 complete winter pelage
January 16-31	4	4 complete winter pelage
February 1-15	3	3 summer pelage on rostrum
February 16-28	8	3 summer pelage on rostrum
		1 entire head in summer pelage
		4 complete winter pelage
March 1-15	4	2 summer pelage on rostrum
		1 summer pelage on head and shoulders
		1 complete winter pelage
March 16-31	12	3 summer pelage on rostrum
		2 head and shoulders molted
		7 complete winter pelage
April 1-15	5	1 head in summer pelage
		1 rostrum in summer pelage
		3 complete winter pelage
April 16-30	5	3 head in summer pelage
		2 anterior half of body in summer pelage
May 1-15	1	1 all summer pelage except flanks
May 16-31	2	2 all summer pelage except flanks

GENERAL HABITS AND BEHAVIOR IN CAPTIVITY

The water shrew appears to be a rather secretive animal remaining under the cover of overhanging banks and debris much of the time. As has previously been discussed, the majority of specimens were secured from traps placed in such situations. During the study I have seen only six individuals alive in the wild. Four of these were along the water's edge under cover of overhanging banks and were observed for only a few seconds before they disappeared. The fifth animal was seen running along the bank of a small stream. It plunged into the water between tree roots, then disappeared. A few seconds later it reappeared, coming out of the water onto the bank at my feet. It started to run along the edge of the bank when it was captured alive by hand. A sixth was observed swimming up the mouth of a small stream several yards wide. It disappeared from sight among the rocks of the stream bank in a few seconds after it was seen.

In habitat where the water shrew was abundant ordinarily no indication of its presence was noted. I have seen tracks on the snow only on one occasion although many specimens have been taken under conditions which would have

made tracks inevitable had the shrews been active upon the surface of the snow. During the winter the habits of the water shrew seem to be as in other seasons, with the majority of the activity confined to banks of streams. In the region where the shrews were collected during the winter, streams do not freeze solid although shelf ice forms along the banks or over the entire stream. When water levels drop a space remains between the bottom of the shelf ice and the water's surface. Many winter specimens were secured along stream banks under such shelf ice.

In one instance four feces were found upon a small rock exposed above water several inches from the edge of an overhanging bank. These feces appeared to be those of a water shrew, so several traps were placed beneath the bank. The next day a specimen was obtained at this site, lending support to the belief that the feces were those of a water shrew. This instance and the one occurrence of tracks are the only occasions upon which any "sign" of the water shrew was found.

The specimen which was captured alive by hand was maintained in captivity between July 12, 1948 and early September 1948, when it died of undetermined causes. This animal was a young male. During the period it remained in captivity it was housed in a ten-gallon aquarium. One to two inches of water was kept in the aquarium with rocks and bark placed in one end to provide a dry area for the shrew. Water was changed five to six times daily, fresh cold spring water being used to refill the aquarium since it was apparent that the shrew became highly agitated whenever the temperature in the aquarium became warm. A small piece of dry cotton was kept on the rocks. This was utilized by the shrew, and it spent much of the time concealed in the cotton although no attempt to construct a definite nest was noted.

The animal was active intermittently during the day and night, but only for short periods. After a period of activity it would retreat to the cotton presumably to sleep before becoming active again. While moving about, it would often simply stop and fall asleep in a crouched position. On several occasions when this happened it was seen to fall from a rock into the water. Davis (1939) states that the water shrew is nocturnal. However, the behavior of the captive specimen, the observation of other individuals during the day, and also the fact that five specimens were known to have been trapped during the day indicates the water shrew is active both during the day and the night.

The behavior of the water shrew in the water and the manner in which it swims has been described by Jackson (1928) and by Svihla (1934) who maintained a specimen in captivity for several weeks. Further elaboration of this seems needless since my observations concur with these descriptions.

Sight seems to be poorly developed while smell and probably tactile senses are important. When small minnows were placed in the water, the shrew would rush about on the rocks, stopping frequently to elevate the nose as if scenting. It would then plunge into the water and swim beenath the surface. If the fish were not moving, the shrew apparently experienced difficulty in

locating them, and it would frequently bump into them seemingly by accident. However, if the fish were swimming, the shrew had little difficulty in finding and following them. This is suggestive that tactile senses might be important under such circumstances.

Svilha (1934) found that his captive animal was unable to capture minnows even after touching them. The specimen I maintained in captivity caught small minnows up to six cm. in length. When eight or ten such minnows were placed in the aquarium, the shrew would capture one in the water and bring it to the rocks. The shrew, using its incisors, would bite the fish through the head to kill it. Usually the first minnow would be eaten immediately. After that, the shrew would continue to catch and kill the fish until none were left. Each one caught would frequently be brought to the same place where it would be killed and deposited; thus a number of minnows would be piled together.

TABLE 6.—Autumn molt in young and old animals

Period	No. of specimens	Condition of molt
July 16-31	7	4 complete summer pelage 2 winter pelage on rostrum 1 winter pelage on rostrum and flanks
August 1-15	5	3 complete summer pelage 2 winter pelage on flanks, back, and rostrum
August 16-31	3	1 complete summer pelage, skin pigmented 1 complete winter pelage except band across top of head 1 posterior part of body in winter pelage.

The remarkable resistance of the water shrew hair to wetting is well known. However, very frequently after several minutes of activity in the water the hair would begin to wet. When this occurred, the animal would dry its fur by rapidly and thoroughly working over its body with the hind feet. During this process fine droplets of water would be thrown off. The process would continue for 10 to 30 seconds after which the hair was dry. The marginal vibrissae of the feet, which are well developed in this species seemed to facilitate this operation, functioning almost as a comb.

The captive specimen was fed largely fish, although it ate dead mice, insects, and any meat offered. It was not seen to eat any vegetable material. During several 24 hour periods an excess of food was placed in the aquarium to determine the quantity which was eaten. For four consecutive days the average food consumption was 10.3 grams of meat or fish for each 24 hour period. Five and one-tenth grams were consumed between 8:30 a.m. and 8:30 p.m. and 5.2 grams between 8:30 p.m. and 8:30 a.m. The body weight of this specimen at the time was probably about ten grams. Food consumption

of various species of shrew has been recorded, and it is well known that daily food intake of some species is greater than their body weight. Thus in a 24 hour period the Turkestan desert shrew, (*Diplomesodon pulchellum*), weighing 10 grams consumed 10 to 17 grams of food (Heptner, 1939); a five gram *Cryptotis floridana* consumed 5.5 grams of food (Springer, 1937); and a captive *Sorex cinereus* consumed 3.3 times its own weight (Blossom, 1932). Svihla (1934) records that his captive *Sorex palustris* ate "a dead *Microtus*, a dead *Zapus*, each of which weighed more than the shrew, besides several snails, all within 24 hours."

During the summer of 1949, three water shrews were trapped in live-traps. One, being in poor condition, died shortly after being removed from the trap. A second animal escaped from a temporary cage shortly after capture. The third individual was maintained for several weeks. The behavior of this animal was essentially similar to that of the specimen previously discussed. However, a spherical nest, composed of moss, was constructed in a hollow tube of tree bark placed in the cage.

On one occasion a living *Sorex vagrans* was placed in the cage with this *Sorex palustris*. Both the *Sorex palustris* and *Sorex vagrans* became highly agitated. Whenever they encountered each other they began to squeak and occasionally fought momentarily. Although neither animal appeared very willing to engage in combat, the wandering shrew seemed more reluctant and attempted to avoid the water shrew. After a period of 15 minutes the wandering shrew was removed with neither animal having suffered harm.

SUMMARY

This study was based upon 119 water shrews taken in Montana, west of the Continental Divide. These specimens were collected with back breaker mouse traps, baited with a mixture of peanut butter and anise oil. The majority of specimens were secured along streams in the Canadian zone at elevations of 2900 to 6950 feet. All specimens were taken very close to the edges of streams and most frequently in traps placed beneath overhanging banks and within a few inches of the water.

A system of age determination based upon measurements of individual teeth to determine tooth-wear was developed. Application of this method indicated that no specimens in the sample had lived beyond the end of the summer following the one in which they were born. Thus the maximum age of any specimen obtained would not be in excess of eighteen months. The standard measurements are given for both sexes of the water shrew.

Male water shrews were not sexually active during the breeding season in which they were born. The following December and January the onset of spermatogenesis began, at which time an increase in body weight was apparent. All males born the previous year taken between January and August were in active spermatogenesis. Pregnant or lactating females were taken between February and August. Ovulation is presumably induced by copulation. A post partum heat occurs, and pregnancy follows in at least some animals. Some animals

which had experienced a post partum heat and ovulation were not pregnant. In these individuals it is thought that resorption of the embryos had occurred at some stage in development.

One young female was pregnant, and two others showed some ovarian activity. The majority of breeding females, however, were old animals born the preceding year. Several litters are produced during the breeding season. The most common number of embryos found was six.

The food of the water shrew is largely insects. Forty-nine per cent of the stomachs examined contained immature forms of aquatic insects. This would indicate that much of the water shrews' food probably comes from aquatic sources. Thirteen species of parasites of the water shrew were found. Dermal glands were found only in sexually active males. Two annual molts occur, one during the spring between February and May, and one in the autumn during July and August.

A specimen was maintained in captivity for seven weeks. This animal was capable of capturing small minnows in the water. The average food consumption of the captive was 10.3 grams of food during a twenty-four hour period.

REFERENCES

BAILEY, V. 1918—Wild animals of Glacier National Park. The Mammals. United States Government Printing Office.

BLOSSOM, P. M. 1932—A pair of long-tailed shrews (*Sorex cinereus cinereus*) in captivity. Journal of Mammalogy 13(2): 136-143.

BORELL, A. E. AND R. ELLIS 1934—Mammals of the Ruby Mountains region of Northeastern Nevada. Ibid. 15(1): 12-44.

BRAMBELL, F. W. R. 1935—Reproduction in the common shrew (*Sorex araneus* Linnaeus). Philosophical Transactions Royal Society of London B 225: 1-62.

———1948—Prenatal mortality in mammals. Biological Reviews of the Cambridge Philosophical Society 23(4): 370-407.

——— AND K. HALL 1937—Reproduction of the lesser shrew (*Sorex minutus* Linnaeus). Proceedings Zoological Society of London 1936: 957-969.

DALQUEST, W. W. 1944—The molting of the wandering shrew. Journal of Mammalogy 25(2): 146-148.

———1948—Mammals of Washington. University of Kansas Publications, Museum of Natural History Vol. 2.

DAVIS, W. B. 1939—The recent mammals of Idaho. Caxton Printers, Caldwell, Idaho.

EADIE, W. R. 1939—A contribution to the biology of Parascalops Breweri. Journal of Mammalogy 20(2): 150-173.

FISHER, R. A. 1938—Statistical methods for research workers. Oliver and Boyd, Edinburgh.

GRINNELL, J. AND T. I. STORER 1924—Animal life in the Yosemite: an account of the mammals, birds, reptiles, and amphibians in a cross section of the Sierra Nevada. University of California Press, Berkeley.

GUYER, M. F. 1936—Animal Micrology. University of Chicago Press, Chicago, Illinois.

HALL, E. R. 1946—Mammals of Nevada. University of California Press, Berkeley.

HAMILTON, W. J. 1930—The food of the Soricidae. Journal of Mammalogy 11(1): 26-39.

———1940—The biology of the smoky shrew (*Sorex fumeus fumeus* Miller). Zoologica 25(4): 473-492.

HAMMOND, J. AND F. H. A. MARSHALL 1925—Reproduction in the rabbit. Edinburgh.

HEPTNER, V. G. 1939—The turkestan desert shrew, its biology and adaptive peculiarities. Journal of Mammalogy 20(2): 139-149.

JACKSON, H. H. T. 1928—A taxonomic review of the American long-tailed shrews. North American Fauna No. 51. United States Government Printing Office, Washington, D. C.

KELSEY, H. P. AND W. A. DAYTON 1942—Standardized plant names. McFarland Co., Harrisburg, Pa.

KOHLS, G. M. 1950—Note on the occurrence of the flea *Nearctopsylla hyrtaci* in the United States. Journal of Parasitology 36(1): 85.

LANPMAN, B. H. 1947—A note on the predacious habits of the water shrews. Journal of Mammalogy 28(2): 181.

LONG, W. S. 1940—Notes on the life histories of some Utah mammals. Ibid. 21(2): 170-180.

PARKES, A. S. 1924—Fertility in Mice. British Journal of Experimental Biology 2(1): 21-31.

PEARSON, O. P. 1944—Reproduction in the shrew (*Blarina brevicauda* Say). American Journal of Anatomy 75(1): 39-93.

———1945—Longevity of the short-tailed shrew. American Midland Naturalist 34(2): 531-546.

———1946—Scent glands of the short-tailed shrew. Anatomical Record 94(4): 615-630.

RAND, A. L. 1944—Mammal investigations on the Canol Road, Yukon and Northwest Territories. Bulletin No. 99, Biological Series No. 28, National Museum of Canada.

SPRINGER, S. 1937—Observations on Cryptotis Floridana in captivity. Journal of Mammalogy 18(2): 237-238.

STIRTON, R. A. 1944—Tropical mammal trapping I: the water mouse, Rheomys. Ibid. 25(4): 337-343.

SVIHLA, A. 1934—The mountain water shrew. The Murrelet 15: 44-45.

WARREN, E. R. 1942—The mammals of Colorado. University of Oklahoma Press. Norman.

Notes and Discussions

Notes on Moraceae and Ulmaceae

In the study of Wisconsin Moraceae and Ulmaceae, there came to light some difficulties in identification due to certain points which it is the purpose of this article to make clearer. To that end, some new forms are proposed.

Apparently a common practice, followed by the writer himself until recently, assigned all elms of this region which had scabrous leaves to *Ulmus rubra* Muhl. (*U. fulva* Michx.). The new edition (8th) of *Gray's Manual* recognizes that two forms of *Ulmus americana* L. have scabrous leaves, but on the other hand does not mention that *U. rubra* sometimes has smooth leaves. In order to clarify the situation, I propose recognizing the smooth-leaved form of *Ulmus rubra* Muhl. as:

f. laevis, nova forma. Differt a specie typica foliis supra laevibus. This form differs from the typical species in having the leaves smooth above instead of scabrous. *Type:* collected in Eau Claire, Eau Claire Co., Wis., by Charles Goessl, No. 1827, 28 July 1915. Specimen in the Milwaukee Public Museum. A specimen in the Gray Herbarium collected by Darlington, 4 June 1852, without locality, is this form.

Since the scabrous quality of the leaves does not distinguish *U. americana* and *U. rubra,* the character of the teeth may be used to identify sterile leafy specimens. *In U. americana,* the leaves are deeply, coarsely toothed with acute teeth. In *U. rubra,* the teeth are finer, shallower, and rather blunt.

A peculiar form of *U. americana* may prove on further study to be a hybrid. Until such time, however, I would designate it as:

U. americana L., **f. viridis,** nova forma. Foliis viridibus exsiccatis obovatis, lateris subequalibus apice attenuato, supra scabris. *Type:* collected at Devil's Lake, Sauk Co., Wis., 6 June 1948, by J. H. Zimmerman, No. 962. Specimen in the herbarium of the University of Wisconsin. In the same herbarium is another specimen of this form, collected 3 miles south of Verona, Dane Co., Wis., by G. Cottam, No. 156. Both of these specimens were identified as *U. fulva* Michx., evidently because of the scabrous leaves. However, the serrations resemble those of *U. americana.* From other forms of *U. americana,* forma viridis differs in the sides of the leaves being almost equal at the base, narrowed at the base, and obovate with attenuate tips. Whereas many specimens of *U. americana* and *U. rubra* turn dark in drying, these leaves characteristically retain a bright green. In the National Herbarium is a specimen of this form collected in Ocean Co., S. C., by H. P. Anderson No. 1119.

In the mulberries, a similar difficulty prevails. Often all mulberries with scabrous leaves appear to have been regarded as *Morus rubra* L., while all with smooth leaves have been treated as *Morus alba* L. So far as my observation goes, the leaves of *M. alba* are never very scabrous, but on vigorous shoots they are often slightly scabrous. In *M. rubra,* on the other hand, the leaves may be either smooth or scabrous. Again, for clarity's sake, the smooth leaved form ought to be given recognition. Therefore, I designate it as:

Morus rubra L., **f. laevis,** nova forma. Foliis laevibus. *Type:* collected at Ferry Bluff, near Sauk City, Sauk Co., Wis., by N. C. Fassett, No. 18625. Specimen in the herbarium of the University of Wisconsin. Specimens of this form are numerous.

The so-called white mulberry (*M. alba* L.) is usually dark-fruited in Wisconsin. This part of the species is commonly known as var. *tatarica* (L.) Ser. Because the distinction between the species and "variety" seems to break down very readily and to be based on very arbitrary measurements, the latter seems scarcely in the rank of a variety. Rehder* gives dimensions to distinguish the dark-fruited from the white-fruited trees, but his measurements of the leaves overlap. As to the color of the fruit, he states that in

* Rehder, Alfred. Cultivated Trees and Shrubs, pp. 188-9.

"var. *tatarica*," it may be either white or "dark-red." To distinguish the fruits by length, he describes those of "var. *tatarica*" as "about 1 cm. long" and those of the typical trees "1-2.5 cm. long." However, I find that small-leaved specimens (which on this basis would be "var. *tatarica*") may have fruit up to 1.5 cm. long. As plants bearing flowers or fruit of a color different from that of the typical are often designated as forms, I propose treating the dark-fruited trees of *Morus alba* as:

f. atropurpurea, novum nomen. (*M. tatarica* L., *M. alba,* var. *tatarica* (L.) Ser.) Fructis atropurpureis.

Another variation of *M. alba* seems worthy of recognition. Usually the hairs on the under side of the leaves are stiff, straight, and spreading at right angles from the veins. A few specimens have hairs that are curved and not spreading. These I designate as:

f. incurva, nova forma. Similis formae atropurpureae sed capillis foliorum subtus incurvis, non passis. *Type:* collected near De Soto, Crawford Co., Wis., by J. J. Davis, 3 Sept. 1932. Specimen in the herbarium of the University of Wisconsin.

Since there has been difficulty in distinguishing *M. alba* from *M. rubra,* it is noteworthy that sterile leafy specimens may be distinguished by the hairs on the under side of the leaves. In *M. alba,* the hairs are confined to the veins, usually the larger veins. In *M. rubra,* the hairs occur abundantly between as well as on the veins. While not wholly reliable, the following characters are helpful. The leaves of *M. rubra* are generally larger (5.5-12 cm. wide), often very scabrous, less often lobed, and longer caudate. In *M. alba,* the leaves are 2.5-6.5 (rarely 11) cm. wide.

To the University of Wisconsin, the Milwaukee Public Museum, the Gray Herbarium, and the National Herbarium, I wish to express appreciation for the privilege of examining their specimens of these species. —FRANK C. SEYMOUR, Tomahawk, Wisconsin.

The Parotid Gland of an Anteater, Tamandua tetradactyla

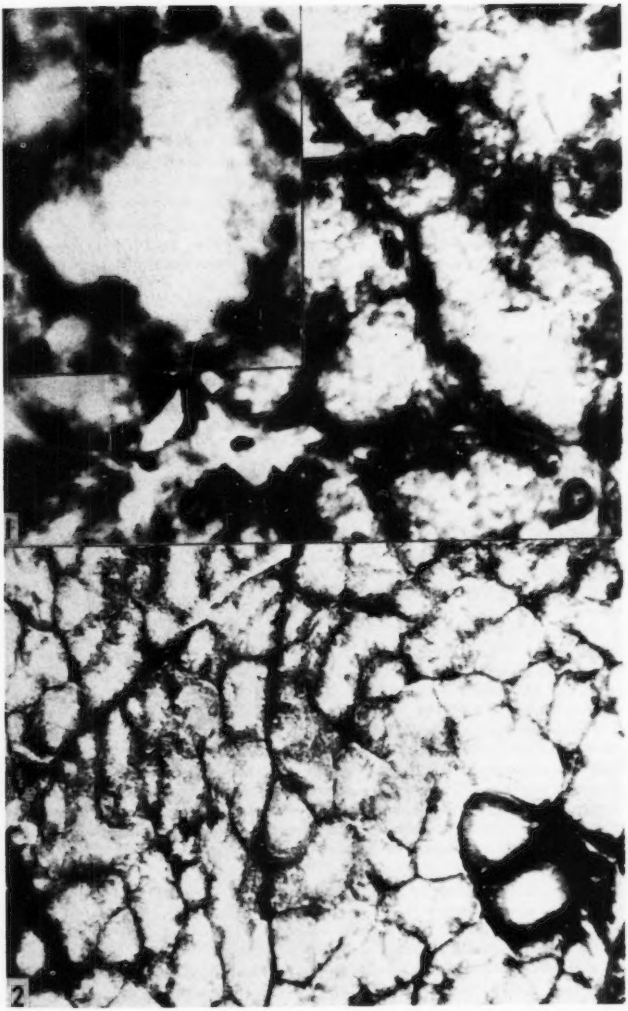
The Central American anteater, *Tamandua tetradactyla,* feeds entirely upon insects. The animal is toothless, and the insects upon which it feeds are entrapped on the sticky saliva of the long tongue, and thus drawn into the mouth and swallowed. The principal source of the saliva is the enormously developed parotid salivary gland. In a freshly killed specimen, taken in southern Vera Cruz, Mexico, the parotid gland extended posteriorly from the corner of the jaw on each side, as a flattened sheet of glandular tissue. This sheet of glandular tissue extended back along the sides of the neck and ventrally over the chest. Lobulation of the gland is visible macroscopically; lobules are about five millimeters in size. When the gland is slashed, it exudes a thick, transparent liquid of about the consistency of Canada Balsam.

Materials and methods.—Sections of the parotid gland of a female *Tamandua tetradactyla* were immediately fixed in 10% formalin for twenty-four hours and then stored in 70% ethyl alcohol. Tissue was dehydrated in ethyl alcohol, cleared in toluene, embedded in parawax, and serially cut at five microns. The following stain techniques were used: Harris' hematoxylin with an alcoholic eosin counter-stain, Mallory's connective tissue stain, and Lillie's iron hematoxylin and metachromatic dye.

Discussion.—The parotid gland of *Tamandua tetradactyla* is a mucous gland. It is surrounded by a connective tissue capsule from which innumerable septa project inwardly, ramifying the substance of the gland, dividing it into lobes and lobules.

The secretory portion of the parotid gland is composed of various sized acini. Each acinus presents the classical picture of a true mucous gland. The typical cell is cuboidal in shape, the nuclei of which are basally situated with their long axes parallel to the basement membrane. The cytoplasm, with an H. and E. technique, is devoid of granules —alveolar in nature (fig. 1). Lillie's selective stain technique demonstrated the presence of mucin within the cytoplasm of each cell.

Considerable difficulty was encountered in sectioning the gland. The tough fibrous



FIGS. 1, 2.—1. Mucous acini with indistinct alveolar-type cytoplasm (×750). Insert (overexposed and undeveloped) enlarged to demonstrate basally situated nuclei (×1500, H. and E. stain); 2. Demonstration of the fibrous connective tissue septa (×175, H. and E. stain).

connective tissue septa (fig. 2) were largely responsible. Their septa evidently serve as a framework of support for an otherwise very soft, pliable gland.

Summary.—The parotid gland of *Tamandua tetradactyla* is a true mucous gland extending posteriorly from the corners of each jaw along the sides of the neck and ventrally over the chest. It is divided into many lobules by penetrating strands of tough fibrous connective tissue. The secretory portion of the gland is made up of mucin secreting acini.—W. W. DALQUEST AND H. J. WERNER, Louisiana State University, Baton Rouge.

Book Reviews

THE FLORA OF BIC AND THE GASPÉ PENINSULA, QUEBEC. By H. J. Scoggan. Bulletin 115, National Museum of Canada, Ottawa. 1950. 399 pp., 8 plates, 1 fig. $1.00.

As stated by the author, Gaspé Peninsula and the region of Bic, together with adjacent areas of eastern Canada, have long been of particular interest to botanists because of the many interesting problems of geographical distribution presented by various elements of the flora. Although the earliest report on the flora of that region was that of John Macoun in 1883, it was the work begun by M. L. Fernald of Harvard University half a century ago that aroused interest in the peculiar botanical phenomena of the region. During a period of thirty years he described nearly 200 new species, varieties, or forms of vascular plants from the region, many of them endemics. This work was augmented by original studies by a number of Canadian botanists, including Marie-Victorin, J. Rousseau, E. LePage, A. E. Porsild, V. C. Wynne-Edwards, and one of his students, H. J. Scoggan.

The question as to whether or not certain parts of the Gaspé Peninsula remained ice-free (forming "nunataks") during the period of maximum Wisconsin glaciation has been for many years a matter of controversy among certain geologists and botanists. The botanist, Fernald, supported by A. P. Coleman, geologist, maintained the affirmative, but Professor Wynne-Edwards of McGill University took an opposite view, pointing out that it is impossible to regard the present flora as having survived many thousands of years in this great province of ice, and his view has been confirmed by later geological studies. Glacial drift has been found up to elevations of 1,800 feet, and a number of well-rounded erratics have been found on the highest part of Mount Albert, indicating that this mountain was buried by ice. Many supposed disjunct ranges of species have been filled in by botanical exploration of parts of western Canada by Porsild, N. Polunin, H. M. Raup, Scoggan and others. Localization of certain species on Gaspé Peninsula is to be accounted for by the close relationship with the soil or rocks upon which they grow. The majority are confined to calcareous or dolomitic soils, while others are strictly serpentine plants in this area. The presence of endemics offers no positive evidence in support of the nunatak theory. Wynne-Edwards believes this phenomenon can be better correlated with the specialized soil preferences of the plants. It seems that the entire flora of the Gaspé Peninsula has migrated from the south with the retreat of the ice, and thus the nunatak theory collapses.

The introductory portion of the book includes, in addition to a discussion of the glacial and post-glacial history of the peninsula, a brief account of the physical features, climate, soil chemistry, biotic factors, affinities of the Gaspé flora, and a tabular classification of families, genera, and species included in the book. A very useful feature is the discussion of life-forms of plants according to the system of Raunkiaer.

Ninety per cent of the book, the systematic portion, consists of carefully prepared dichotomous keys and annotated lists of the 1216 species and about 250 varieties and forms. The 418 genera are included in 97 families. There are 67 species of pteridophytes, 11 species of gymnosperms, and 332 monocotyledons. Under the name of the genus reference is often made to recent or otherwise significant systematic studies. Following the name of the species is the symbol for the life-form, habitat, localities where

specimens have been collected, and a statement of geographical origin and distribution of the species. The taxonomy and nomenclature perhaps quite naturally, show a certain amount of influence from *Gray's Manual*, although it is gratifying to find white baneberry as *Actaea alba*, wild red raspberry as *Rubus strigosus*, cowparsnip as *Heracleum lanatum*, and garden snowberry as *Symphoricarpos rivularis*. Following Fernald, who in turn was attempting to follow DeCandolle, Dr. Scoggan merges *Sorbus* and *Aronia* with *Pyrus*, hence the American mountain-ash is named *Pyrus americana* (Marsh.) DC., but a fact pointed out in *Journ. Arnold Arboretum* 20:16, 1939, apparently has been overlooked, namely that in 1825 when DeCandolle transferred species of *Sorbus* to *Pyrus*, "unfortunately the name *Pyrus americana* DC., designating the northern shrub with acute leaflets and large fruits is based upon *Sorbus americana* Pursh, and therefore is not synonymous with *S. americana* Marsh."

Not only is Dr. Scoggan to be congratulated on having produced a thorough and successful study of the flora of this region, but the National Museum of Canada is to be commended for the attractive job of publication of this work at such a low price.—GEORGE NEVILLE JONES, University of Illinois, Urbana.

AN INTRODUCTION TO PLANT SCIENCE. By W. W. Robbins and T. E. Weier. John Wiley and Sons, Inc. New York. 1950. 480 pp., 490 illus. $5.00.

In writing this textook the authors have made a very special effort to attract the interest of the student. To this end, they have organized their presentation of the basic facts of botany in such a way as to get and hold his interest. They initiate the student to the subject matter by showing him how it affects him in his daily life, what it contributes to his livelihood and how it is generally related to the other sciences.

The text covers the general subject of botany in the traditional manner. The plant and its essential organs are presented first, followed later by the classification of the plant kingdom. The selection of the discussion of the plant as a whole prior to the study of the plant kingdom is in accord with modern techniques and contributes much to maintain interest. This order tends to acquaint the student more gradually with the use of new terms and the acquisition of a scientific vocabulary. Very commendable is the practice by the authors of defining new technical terms when they appear for the first time.

One of the outstanding good features of this text is its organization, not only is the subject matter ably, clearly and stimulatingly presented but the nearly 500 well-chosen illustrations are unusually large, sharp and conveniently placed close to the subject matter under discussion. The double column format is particularly well adapted to this arrangement. The student thus can see an illustration of what he is reading and almost always on the same page—in clear-cut line drawings, photographs and photomicrographs.

After a good trial, I find this an excellent text, ably written and well organized. It is full of well-chosen illustrations and relatively free of controversial details in the subject matter. It tends to sustain the interest of the reader throughout—a fact not lessened by the good printing and the double column format. I am using this text in some of my own elementary botany sections.—A. L. DELISLE, University of Notre Dame, Notre Dame, Indiana.

A NATURAL HISTORY OF TREES OF EASTERN AND CENTRAL NORTH AMERICA. By Donald Culross Peattie. Houghton Mifflin Company, Boston, Mass. 1950. xv+606 pages. illus. $5.00.

According to the foreword, this book is the first in a contemplated series on the trees of North America north of Mexico, other volumes by the same author to appear later. The region covered in the first volume is indicated roughly on an outline map of northeastern North America decorating the pages inside the front and back covers.

In a short section headed "Notes on Nomenclature," the author states that he has

endeavored to apply the Rules of the International Code. The text considers 153 species native to North America, most of which are strikingly illustrated with one or more black and white figures drawn by Paul Landacre.

In his characteristic easy style, which makes the book as much of literary as of botanical interest, Mr. Peattie has incorporated factual information about the trees along with interesting folklore. Preceding the main discussion of each species is a short description of the range and a non-technical description of distinguishing characteristics. These paragraphs, printed in smaller type, and the Keys to the Species and Genera in the back of the book, are subordinate to the author's real purpose, which is to tell of the things by which a tree "has made history, or witnessed it, or entered into our folkways, or usefully become a part of our daily life."

It is evident that considerable research has entered into the unearthing of so many facts of varying nature about individual species. Some are related primarily from the standpoint of historical interest, such as for the White Pine. Here twelve pages are devoted to a discussion of *Pinus Strobus*, which was, according to history, "one of the chief economic and psychological factors in the gathering storm of the American Revolution." Other facts, such as those of medicinal interest, are told of certain species such as the Sassafras, the roots of which "were grubbed out by the ton" for the production of the oil. Many more are considered from the standpoint of commercial importance, whether used for lumber, paper pulp, fence posts, or for pencils, as for example the red cedar, which bore the brunt of the attack of pencil makers for more than a century.

Attention is called to the virtual extinction of certain species through the wanton destruction of our forests, to the need for conservation practices, and to the recreational value of many of the trees. The book contains a great deal of interesting information, designed primarily for the layman, with "an invitation to explore the woods" for himself. It adds another volume to Mr. Peattie's already impressive list of works on natural history, a book for naturalists by a naturalist.—H. E. AND VIRGINIA BAILEY, Wayne University, Detroit, Michigan.

AMERICAN SOCIAL INSECTS, A BOOK ABOUT BEES, ANTS, WASPS, AND TERMITES. By Charles D. Michener and Mary H. Michener. D. Van Nostrand Co., New York. 1951. xiv+267 pp. $6.00.

It is not usual for a book written primarily for non-technical readers to contain such a background of sound scientific material as Professor and Mrs. Michener have woven into their *American Social Insects*. The book is filled with fascinating material narrated in a delightfully intelligible manner. In popularizing their subject they have not fallen into the common error of humanizing the insects. A series of 26 chapters, most of them not over 20 pages and many 10 pages or less, permits the treatment of individual topics as small, easily grasped units. No reviewer could avoid mention of the excellent photographs, many of which are in natural color.

The book is not a mere random compilation of interesting but unrelated facts. Conditions in the various groups of Hymenoptera are interpreted and integrated into a sound biological unity. While the technical material dispersed throughout is gratifying to the scientific reader, it is so unobtrusively added that it should not disturb but rather stimulate the popular reader to further reading.

Terms are clearly defined. Reactions of insects are explained as interaction of instincts and learning to determine the behavior. Sex, which is basic in development of insect societies, is explained briefly in terms of genetics. The origin and development of social relations are traced to show how insect societies are developed around the family relationships with parthenogenetic reproduction at the lower end of the scale and intricate patterns of parental care at the opposite extreme.

The recent investigations of von Frisch, interpreting the language of the honeybees, are reviewed briefly showing how the returning worker, loaded with nectar, is able by bodily movements and activity to convey to other workers in the hive the actual direction, distance and nature of the nectar supply that she located.

It is only natural that popular interest in honeybees and ants, stimulated by the earlier works of writers such as Fabre and Maeterlinck and numerous more recent popularizations, should dictate extended treatment of these insects.

Throughout the book there is a sound background of morphology in its relation to function but a glossary and a very brief appendix offers a summary of the essentials of insect structure and the broad classification of the Hymenoptera to supplement the information available to the non-technical reader.

This volume is indeed a worthy addition to the series of "The New Illustrated Naturalist."—HARLEY J. VAN CLEAVE, University of Illinois, Urbana.

ZWISCHEN ATLANTIK UND PAZIFIK ZOOLOGISCHE REISESKIZZEN AUS NORDAMERIKA. By Robert Mertens. Alfred Kernen, Stuttgart. 1951. 160 p., illus. DM 9.50 [about $2.30].

It could scarcely have been predicted that it would require a visitor from abroad to bring to American herpetologists a renewed enthusiasm for their own subject material. This is Dr. Merten's message to us—at least to me. His unbounded enthusiasm at catching prairie gartersnakes (*Thamnophis radix* to him) in Mr. Inger's backyard in Homewood, or cricket frogs at the Illinois River Laboratory of the Illinois Natural History Survey, was a delight to the herpetologist's heart. Most of the American herpetological fauna was so well known to him by scientific name, that almost every species seen was either a "first time seen" or a "first time seen alive," and he conveys something of the respect for the herpetological interest of the North American herpetological fauna that our amphibians and reptiles well deserve.

Dr. Mertens is Director of the Museum of the Senckenbergische Naturforschende Gesellschaft in Frankfort a/M., and professor of zoology in the University in that city. At least informally, he was a part of the exchange of personnel between the University of Chicago and the Johann Wolfgang Goethe Universität, inaugurated as a step toward the post war re-establishment of international relations in the world of scholarship. I had the great pleasure of spending three months in the following year at Frankfort as counterpart of this exchange, and quite as the Chicago Natural History Museum was headquarters for Dr. Mertens, I had a pleasant workroom in the Senckenberg Museum throughout my stay in Frankfort.

Dr. Merten's little book makes a most charming herpetological guide book for a herpetological tour of the United States. It is perhaps desirable to call attention to his two earlier separately published books—*Aus dem Tierleben der Tropen*, 1940 (see COPEIA, 1948:149), and *Die Tierwalt des tropischen Regenwaldes* (1948).—KARL P. SCHMIDT, Chicago Natural History Museum, Chicago.

THE CHORDATES. By Herber W. Rand. The Blakiston Co., Philadelphia. 1950. xi+ 862 pp., 609 figs. $6.00.

The plan of Dr. Rand's new book allows presentation of comparative chordate anatomy in a logical order. Part I describes the basic structure of the vertebrates before the two chapters on reproduction and histology. In Part II are two chapters of a historical and theoretic nature. A comparative description of all chordates, including material on comparative embryology, comprises Part III. This sequence is based on the tenet that a "mere knowledge of facts has little value." Added to its content of anatomic fact is some knowledge of the history of anatomy, some account of embryonic development, and an appreciation of the human import of the study from the fishes and amphibians to the mammals. This excellent text is well adaptable to a year's course in comparative anatomy, or as an invaluable reference work in shorter courses.—B. J. JASKOSKI, Creighton University, Omaha, Nebraska.

HANDBOOK OF FRESHWATER FISHERY BIOLOGY. By Kenneth D. Carlander. Wm. C. Brown Company, Dubuque, Iowa. 1950. v+281 pages and appendix. $4.50.

The scope of this handbook is chiefly limited to tabulated information on age and growth (length and weight measurements) studies of fresh-water fishes of United States and Canada. Some statistics on populations and egg production are included.

Data from over 1000 articles have been compiled into neatly arranged tables covering 212 pages of the handbook. Various codes are used in order to conserve space; none of which detract from the usefulness of the tables. It seems unnecessarily confusing to have the standard lengths recorded in millimeters and the fork and total lengths in inches. However, for the convenience of the reader, additional tables are placed in the back of the book for converting inches to millimeters, ounces to grams, etc.

The book is not completely free from typographical errors and the tremendous task of compiling and summarizing extensive data has resulted in various discrepancies. The original references of a dozen titles listed in the author's extensive bibliography were consulted and checked against the tables in the handbook. (1) Page 85, *Hypentelium nigricans*, Age Group IX is actually Age Group XI and the information on Age Group IX is omitted. (2) Page 58, shallow water cisco, the title for Age Group VI is omitted —making it impossible to distinguish between two age groups. (3) Page 59, shallow water cisco, opposite B-79 Mich. Swain L. and under the column entitled No. should read 28 and not 29.

The short section entitled, "Suggestions for Conducting a Sample Age and Growth Study" is well written, but the task of expanding this book into something more than a handbook of statistics on fishes seems too ambitious. It would be more advantageous if the author emphasized greater coverage of important statistics published on fishes. Possibly studies on food habits, chemical and physical tolerances, and biotic conditions could be added.

The handbook should not be used in lieu of original papers. Nevertheless, it is an excellent aid in locating statistical data on fishes, summarizes and compiles scattered information into relatively few tables, and gives a general understanding of the extent of knowledge in respect to age and growth of fresh-water fishes.

A list of the sources of information (with inclusive dates) which were consulted by the author would be helpful.

Dr. Carlander has made a definite contribution to the study of fishes. This handbook should prove useful to most individuals interested in fresh-water fishes. Its future use depends upon how complete, accurate and current it is possible to maintain a book of this nature. It is hoped that the author will be encouraged and find it profitable to continue his efforts.—CLARENCE F. DINEEN, University of Notre Dame, Notre Dame, Indiana.

PRACTICE OF WILDLIFE CONSERVATION. By Leonard W. Wing. John Wiley & Sons, Inc. New York. 1951. viii+412 pp., illus. $5.50.

Dr. Wing's book is intended as a textbook for college students in conservation. This function it will serve admirably. However, it is more than a textbook, for its readability and general treatment of the topic are of the type that should be placed in the hands of sportsmen and the general public.

In this volume the author has integrated the necessary basic biological knowledge, field investigation and practice techniques, management, state and federal powers and controls, and administrative aspects into a meaningful picture of animal conservation. As the author states in the preface, the object was to "blend the theoretical and scientific aspects with actual field practice along lines that experience has shown to be desirable and workable. In so doing, the book considers the land picture existing today, after man has interjected himself into it."

There is no bibliography as such, but at the end of each chapter is a selected list of suggested readings to which the interested person may go for more information. Illustrations are well chosen, the format is pleasing, and the printing is of high quality.—R. L. LIVEZEY, University of Notre Dame, Notre Dame, Indiana.